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MONOGRAPH OF THE NEOTROPICAL SPECIES OF *ASPLENIUM* SECT. *HYMENASPLENIUM* (ASPLENIACEAE)[1]

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Abstract

Asplenium sect. *Hymenasplenium* is one of the best defined groups of *Asplenium*, being characterized by creeping rhizomes, dorsiventrally symmetrical steles, swollen petiole bases, unique rachis-costae structure, and chromosome base numbers of $x = 38$ or 39. In the Neotropics, the section has ten species and three hybrids. The species are *A. delitescens*, *A. hoffmannii*, *A. laetum*, *A. obtusifolium*, *A. ortegae*, *A. purpurascens*, *A. repandulum*, *A. riparium*, *A. triquetrum*, and *A. volubile*. The hybrids are *A.* ×*papyraceum* (of unknown parentage), *A. delitescens* × *A. laetum*, and *A.* ×*incisoserratum* (= *A. hoffmannii* × *A. laetum*). All the aforementioned species and hybrids are endemic to the Neotropics. Central America and the Andes harbor the most species and endemics. A cladistic analysis was not done because the neotropical species of the section apparently do not form a monophyletic group separate from the paleotropical ones.

Section *Hymenasplenium* is one of the best defined groups within *Asplenium*, distinguished by the following synapomorphies: creeping rhizomes, dorsiventrally symmetrical steles, swollen petiole bases, unique rachis-costae structure and chromosome base numbers of $x = 38$ or 39. All other *Asplenium* species have erect or ascending rhizomes, radially symmetrical steles, nonswollen petiole bases, and $n = 36$ or multiples thereof (rare exceptions differ in only one of these characteristics).

Hymenasplenium was first described by Hayata

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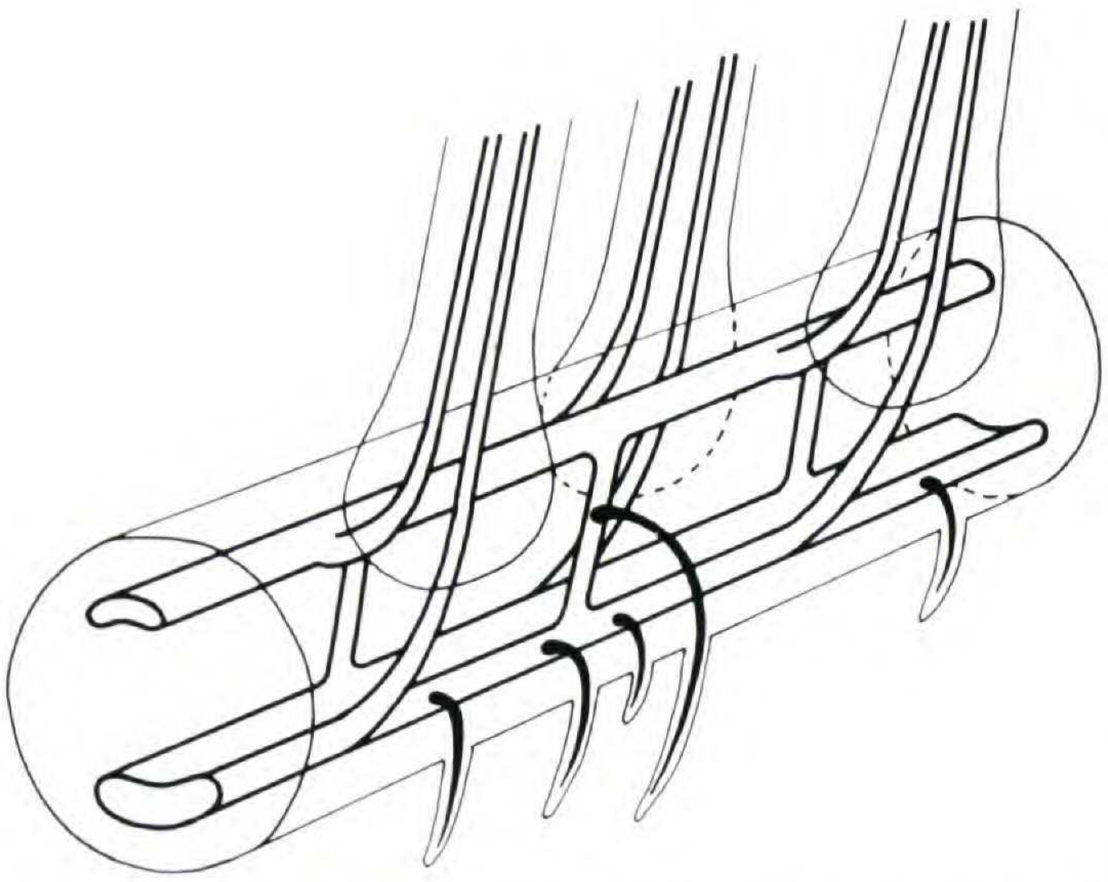

FIGURE 1. Creeping rhizome, dorsiventral stele, and swollen leaf bases—characteristics of *Asplenium* sect. *Hymenasplenium*.

(1927) as a monotypic genus based on *A. unilaterale* Lam. and distinguished entirely by the stelar structure of the long-creeping rhizome (Fig. 1). Hayata was greatly influenced by stelar structure and described several genera based solely upon this character (e.g., *Diploblechnum*, *Monachosorella*, *Boniniella*, *Pentarhizidium*, and *Hymenasplenium*). Iwatsuki (1975) revised the species of *Hymenasplenium*, which were then thought to occur primarily in the Old World, and reduced the genus to a section of *Asplenium*. This ranking has been followed by nearly all pteridologists, including us.

The present monograph treats 10 neotropical species that clearly belong to section *Hymenasplenium* alongside the Old World species. (The Old World species of the section are *A. apogamum* Murakami & Hatanaka, *A. cardiophyllum* (Hance) Baker, *A. cataractarum* Rosenstock, *A. cheilosorum* Kunze, *A. excisum* C. Presl, *A. hondoense* Murakami & Hatanaka, *A. obliquissimum* (Hayata) Sugimoto & Kurata, *A. obscurum* Blume, *A. subnormale* Copel., and *A. unilaterale* Lam.) We have not done a cladistic study of the neotropical species because they are not a monophyletic group distinct from the paleotropical species. The first author plans to do a cladistic study of all the species in the section worldwide using evidence from morphology, anatomy, chloroplast DNA, and nuclear gene sequencing of the small subunit of ribulose-bis phosphate carboxylase. The only difference we have seen between the Old and New World species is that the New World ones have proliferous roots, whereas the Old World ones do not. Proliferous roots do not correlate with any other character (besides geography) and therefore cannot be used to define a natural group.

Previous workers, studying only the Old World species of section *Hymenasplenium*, have surveyed anatomy (Iwatsuki & Kato, 1975; Misuta et al., 1980), reproductive patterns and morphological variation (Murakami & Iwatsuki, 1983), phytochemistry and chemotaxonomy (Murakami & Hatanaka, 1983, 1985, 1988a; Murakami et al., 1985), ecology and morphological variation (Kato & Iwatsuki, 1985, 1986), genetic diversity (Watano & Iwatsuki, 1988), taxonomy (Murakami & Hatanaka, 1988b), and chromosome numbers (Mitui et al., 1989).

The New World species are much more poorly studied. For a long time, workers in the Old World thought that the only New World species that belonged to section *Hymenasplenium* was *A. obtusifolium*. Smith (1976) was the first to point out that the New World species *A. delitescens*, *A. melanopus* (= *A. purpurascens*), *A. laetum*, *A. hoffmannii*, and *A. repandulum* also belonged to the section. He did not, however, study the group in detail.

SPORES

We examined the spores of all the neotropical species of section *Hymenasplenium* and found that perispore morphology was useful in defining two groups. The first group has five species, which we informally refer to as the "*repandulum* group." It comprises *A. obtusifolium*, *A. repandulum*, *A. riparium*, *A. triquetrum*, and *A. volubile*. All have spiny spores (Fig. 2A–C) or, in the case of *A. obtusifolium*, papillate spores (Fig. 2G, H). The second group comprises the rest of the neotropical species, which all have cristate spores (Fig. 2D–F). The eight paleotropical species of section *Hymenasplenium* examined by Kato et al. (1990)

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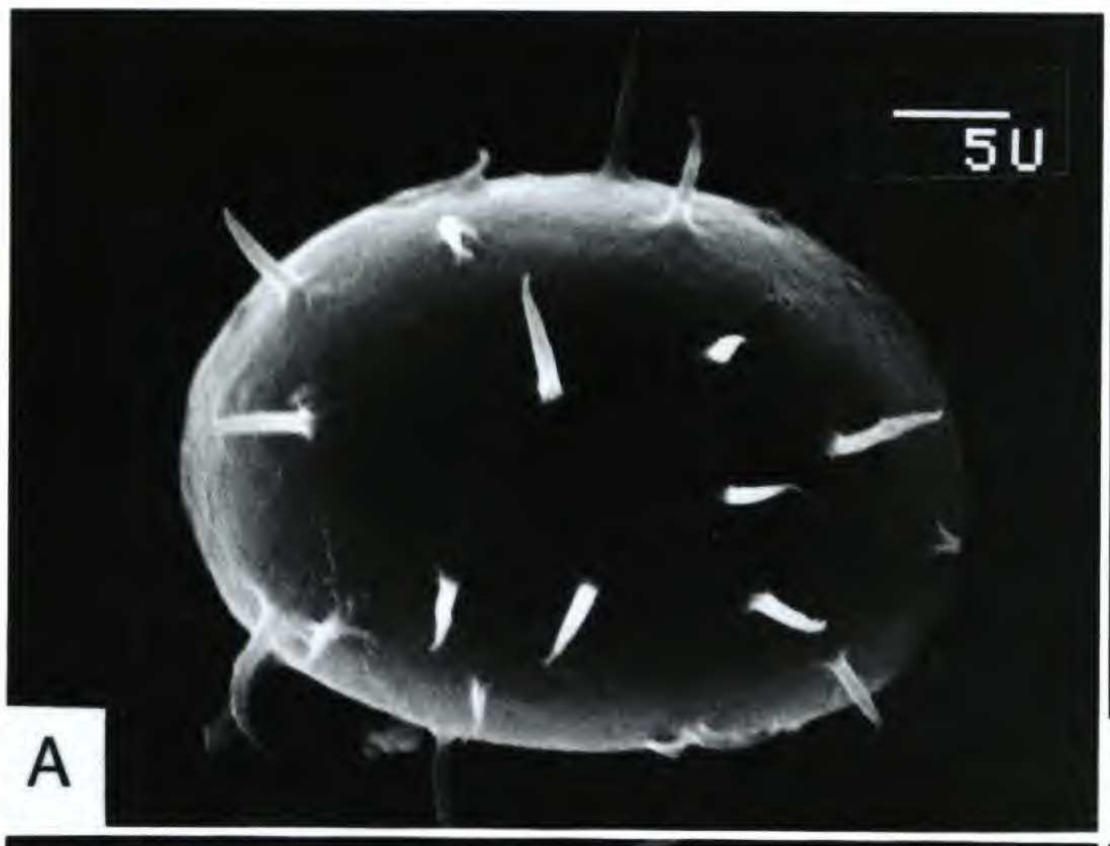
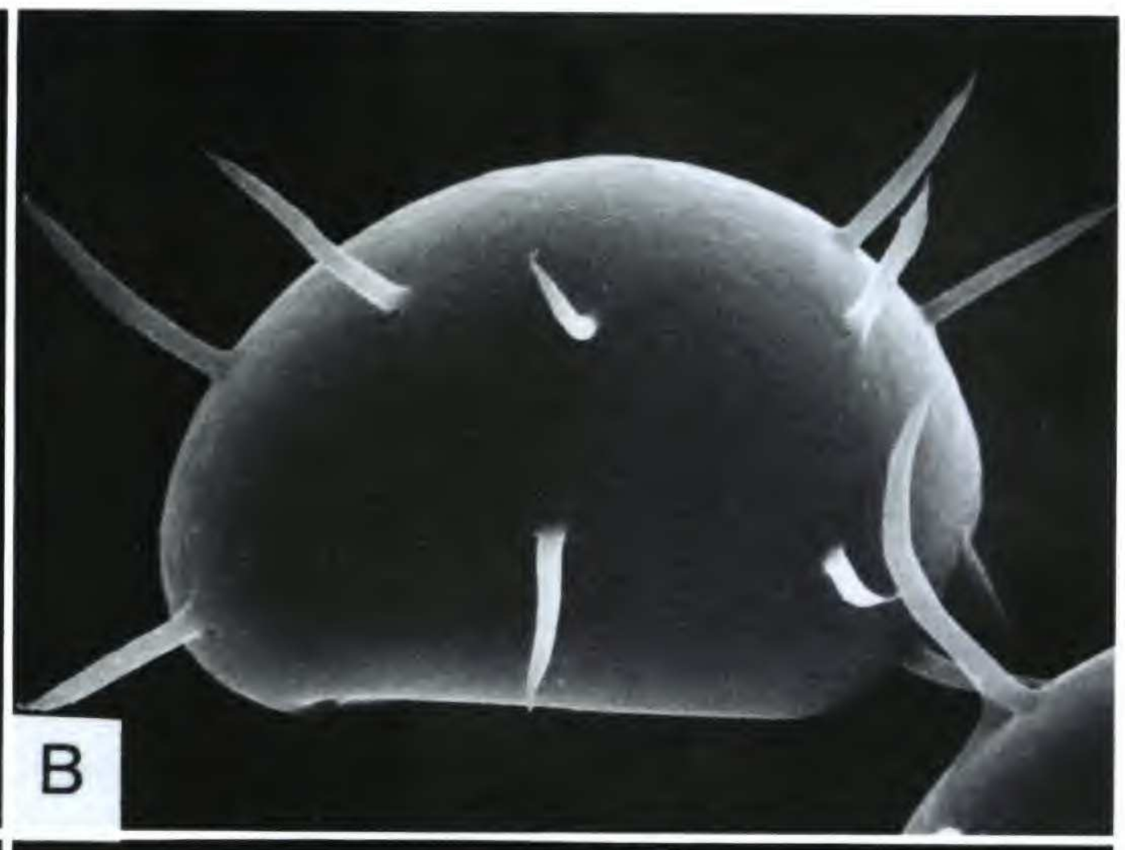
FIGURE 2. The spores of various neotropical species of *Asplenium*, sect. *Hymenasplenium*.—A. *A. riparium*, Mexico, *Copeland 15940* (MICH).—B. *A. volubile*, Colombia, *Forero et al. 7237* (F).—C. *A. repandulum*, Ecuador, *van der Werff 660* (GH).—D. *A. hoffmannii*, Panama, *Johnston 258* (GH).—E. *A. ortegae*, *Steyermark et al. 127134* (UC).—F. *A. delitescens*, Brazil, *Sperling 6035* (UC).—G. *A. obtusifolium*, race with 32 spores per sporangium, Panama, *Antonio 3530* (MO).—H. *A. obtusifolium*, race with 64 spores per sporangium, Venezuela, *Steyermark et al. 121451* (UC).



A



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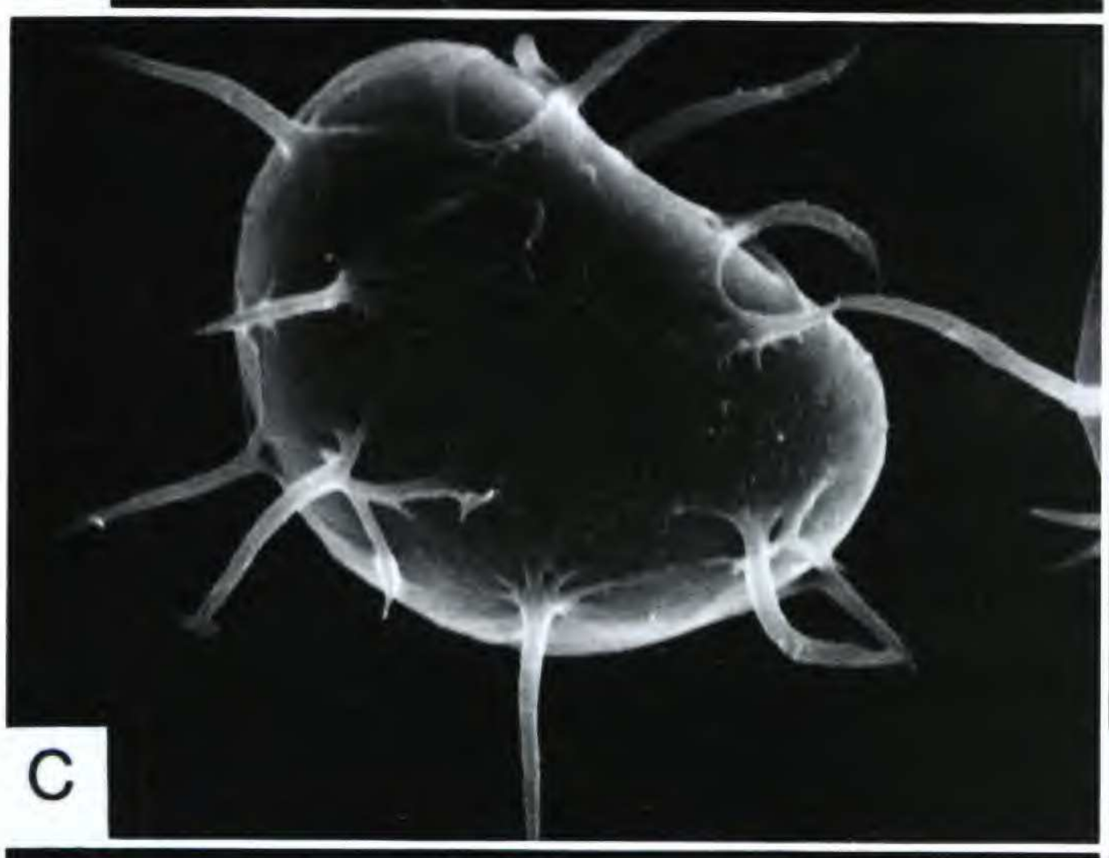
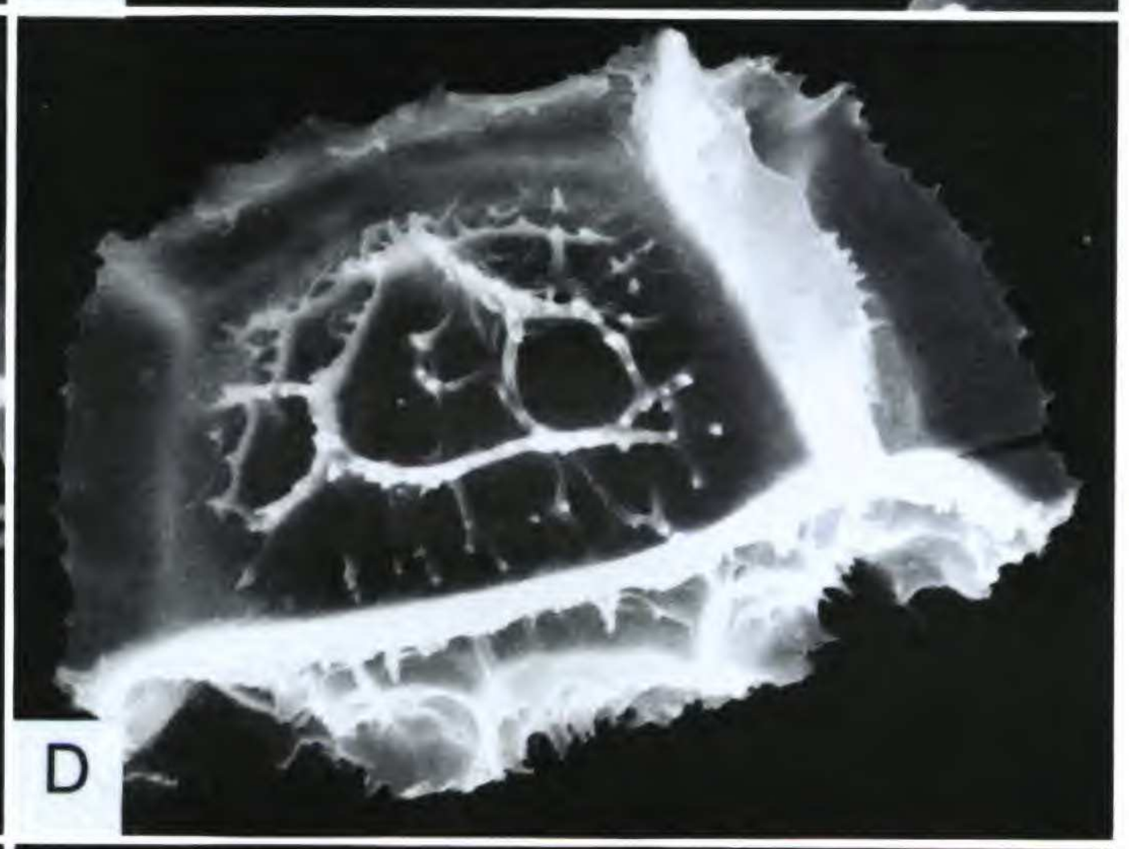


C



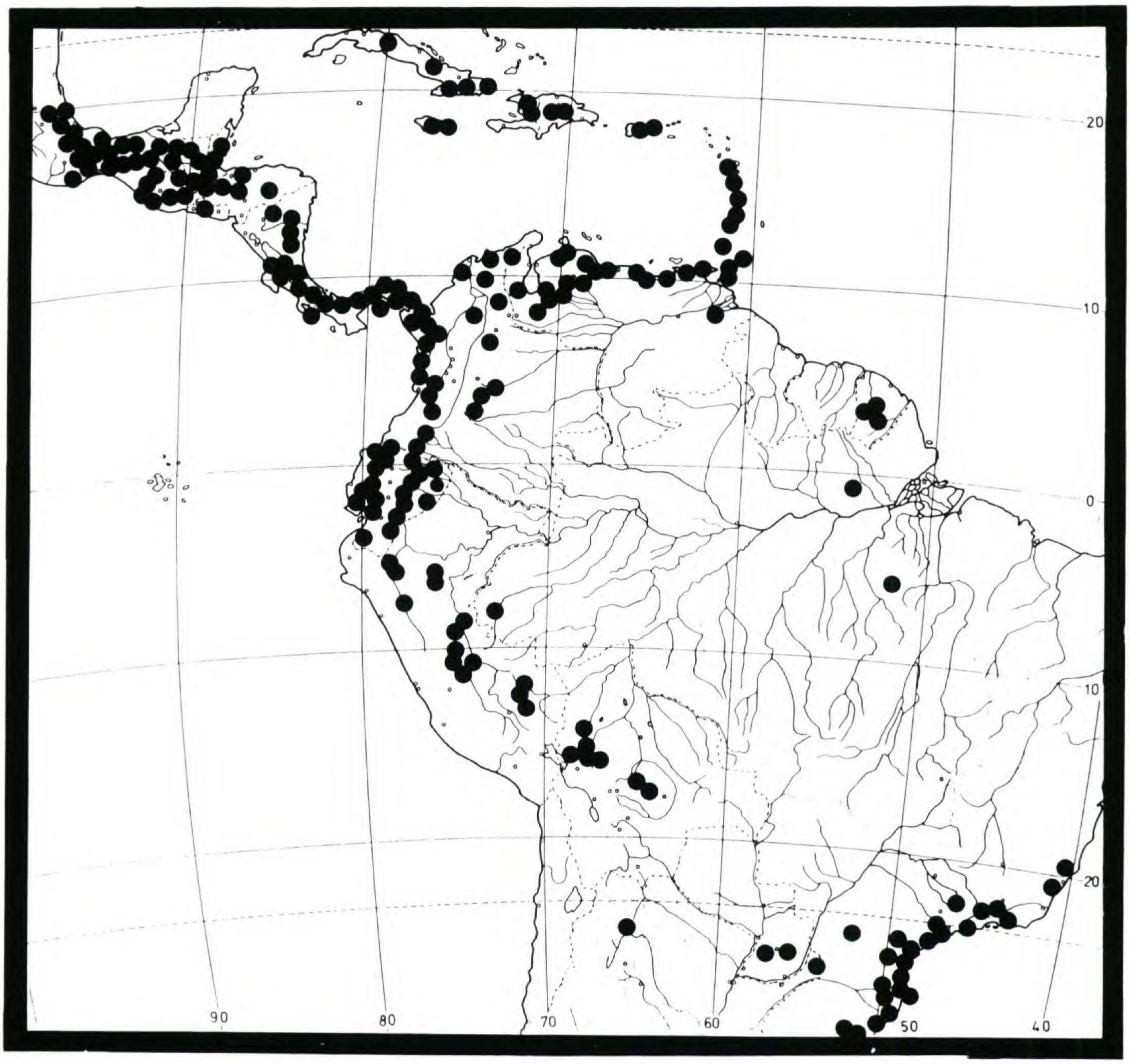
D

E

F

G

H



MAP 1. The distribution of *Asplenium* sect. *Hymenasplenium* in the New World.

had cristate spores and would therefore belong to this second group. Because most species of *Asplenium* outside of section *Hymenasplenium* have cristate spores (Tryon & Lugardon, 1991), the spiny and papillate character states should be considered apomorphic.

GEOGRAPHY

The neotropical species of section *Hymenasplenium* are all endemic to the Neotropics. They range from southern Mexico to Panama, the Antilles, and South America from Venezuela to southeastern Brazil, forming a wide arc around most of Amazonian Brazil (Map 1).

The Andes from Venezuela to Bolivia harbor the most species (8) and this is the only region with endemics (i.e., *Asplenium ortegae*, *A. repandulum*, *A. volubile*). Costa Rica and Panama are also species-rich, containing six species. The Antilles and extreme western Amazonian Brazil both have two species, and the Guianas, southeastern Brazil, and Paraguay all have one species. The Serra do Mar region of southeastern Brazil, which is a center of species richness and endemism for ferns (Tryon, 1972), has played a minor role in the diversification of the section. Only one species (*A. triquetrum*) occurs there and it is nearly endemic (Map 9).

Asplenium obtusifolium is notable for its nearly circum-Caribbean distribution (Map 5) and its correlation with geography of the 32- and 64-spored races.

PRINCIPAL COMPONENTS ANALYSIS

Our recognition of 10 neotropical species of *Asplenium* sect. *Hymenasplenium* is based primarily upon qualitative characters as shown in the key. In order to check the validity of our species circumscriptions, we decided to do a Principal Com-

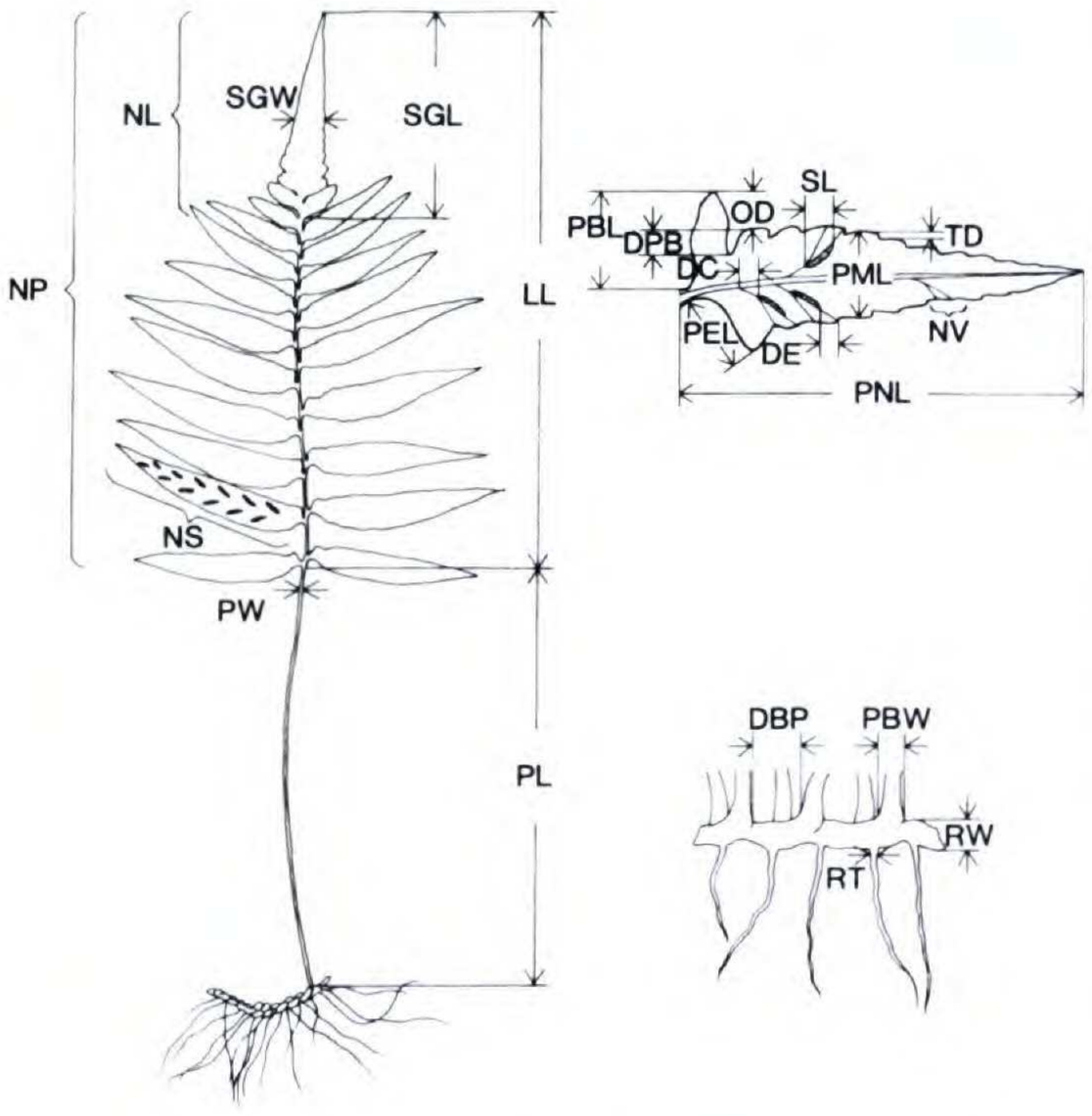


FIGURE 3. Parts of the plants measured for the Principal Components Analyses (Figs. 4, 5). Lamina length (LL), petiole length (PL), petiole width (PW), number of pinna pairs (NP), pinna length (PNL), pinna base length (PBL), pinna width at middle (PML), pinna excised portion length (PEL), number of veins (NV), depth at pinna base (DPB), auricle length (OD), serration depth at tip (TD), number of sori (NS), sorus length (SL), distance to sorus from edge of pinna (DE), distance from costa (DC), segment length (SGL), segment width (SGW), number of lobes (NL), rhizome width (RW), petiole base width (PBW), distance between two petioles (DBP), root width (RT).

ponents Analysis (PCA) of certain quantitative characters (Fig. 3) measured on herbarium specimens throughout the range of each species. We separated the species into two groups according to their separation in the first couplet of the key. The first group, which is identified under lead 1b in the key, contained *A. hoffmannii*, *A. laetum*, *A. delitescens*, *A. purpurascens*, and *A. ortegae*. The second group, which we believe to comprise a closely related group of species and which is identified under lead 1a of the key, contained *A. obtusifolium*, *A. repandulum*, *A. riparium*, *A. volubile*, and *A. triquetrum*. Then, we did a PCA on each group using computer program NTSYS version 1.40 (Rohlf, 1988). The data set for each herbarium specimen was projected on three principal component axes for the first group (Fig. 4) and two axes for the second group (Fig. 5; the third axis accounted for little variation in the second group). Tables 1 and 2 show the Eigen values and Eigen vectors of the Principal Components.

The result for the first group was that all species were separated from each other (Fig. 4). This result supports our circumscriptions of the species.

The result for the second group was not as clear (Fig. 5). Although *A. obtusifolium*, *A. riparium*, and *A. volubile* were separated from each other, *A. repandulum* completely overlapped *A. triquetrum* and *A. volubile*. *Asplenium repandulum*,

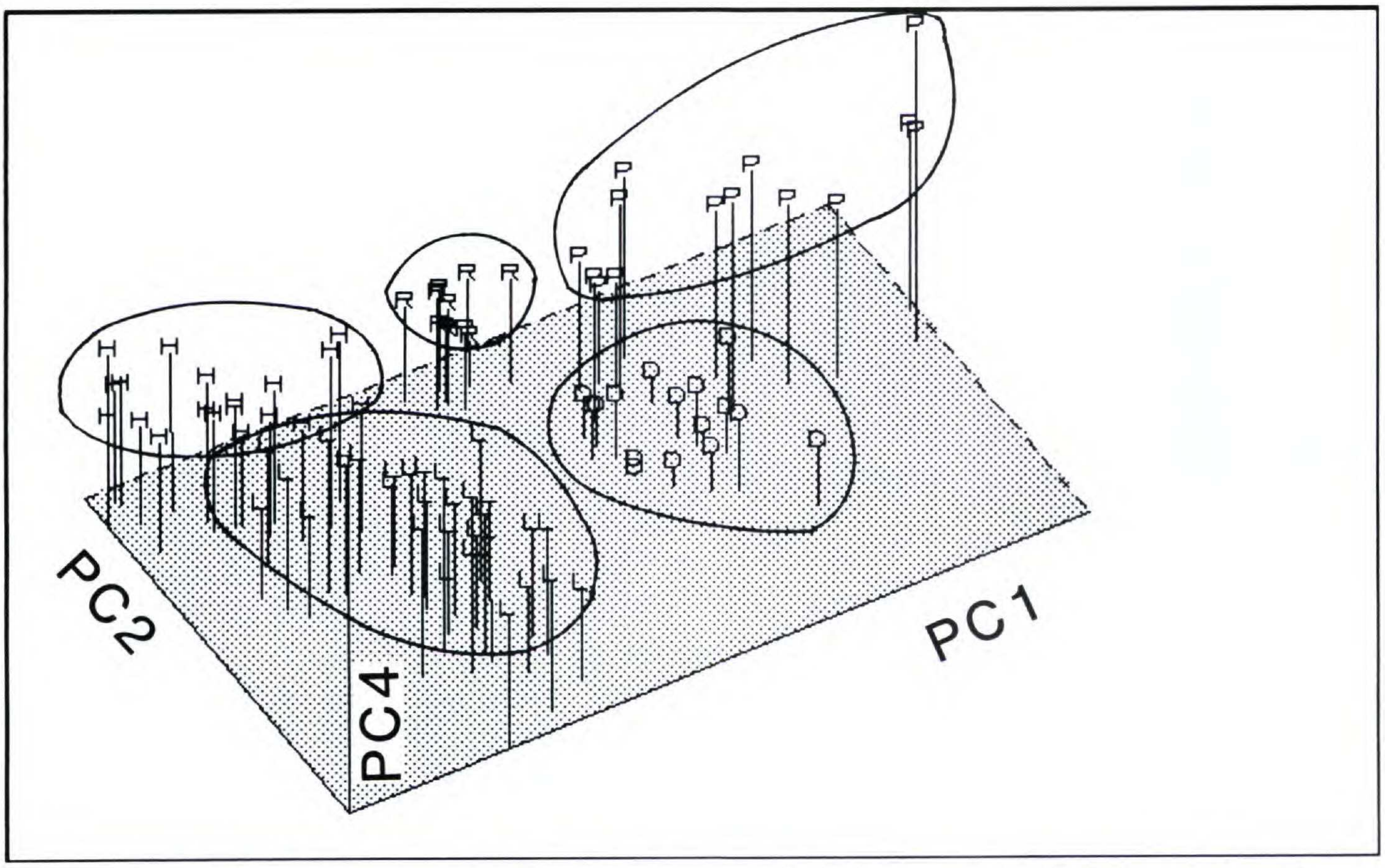


FIGURE 4. Principal Components Analysis of 23 characters of *A. delitescens* (D), *A. hoffmannii* (H), *A. laetum* (L), *A. ortegae* (R), and *A. purpurascens* (P). The three Principal Component axes account for 62% of the measured variation.

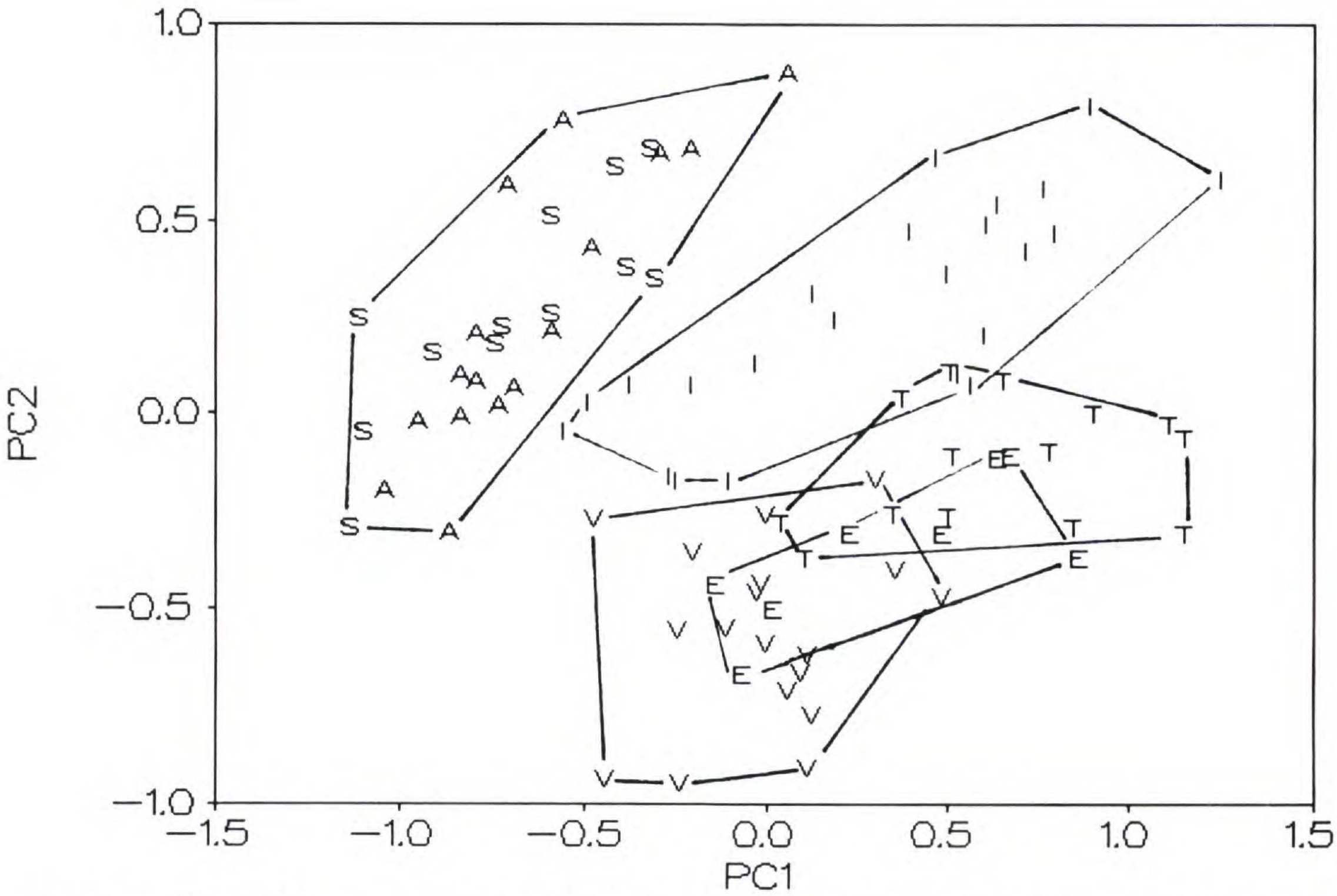


FIGURE 5. Principal Components Analysis of 20 characters of *A. obtusifolium* (A, 32-spored race; S, 64-spored race), *A. repandulum* (E), *A. riparium* (I), *A. volubile* (V), and *A. triquetrum* (T). The two Principal Component axes account for 54% of the measured variation.

however, can be distinguished from *A. triquetrum* by petiole length relative to the lamina, habitat, and range (see key, couplet 4), and from *A. volubile* by the carinate rachis and rachidial wings parallel to the plane of the lamina. These characteristics were not included in the measurements used for the PCA. Another result was that the two spore-races of *A. obtusifolium* could not be separated by the morphological characteristics measured (Fig. 5).

RELATIONSHIP TO OTHER GROUPS OF *ASPLENIUM*

We are not sure what group of species within *Asplenium* is most closely related to section *Hymenasplenium*. Several species of *Asplenium* (*A. abscissum* Willd., *A. argentinum* Hieron., *A. hostmannii* Hieron., and *A. otites* Link) greatly resemble certain species in section *Hymenasplenium* in leaf form. Consequently, they are often misidentified as a species in section *Hymenasplenium*, especially *A. laetum* (which see for comparison). These species, which can be immediately distinguished from section *Hymenasplenium* by their erect rhizomes and rachis-costa architecture, may be the closest group in *Asplenium* related to section *Hymenasplenium*. This suggestion is based only on similarities in leaf form and is therefore tentative.

TAXONOMIC TREATMENT

Asplenium sect. **Hymenasplenium** (Hayata) Iwatsuki, Acta Phytotax. Geobot. 27: 44. 1975. Basionym: *Hymenasplenium* Hayata, Bot. Mag. (Tokyo) 41: 712. 1927. TYPE: *Asplenium unilaterale* Lam.

Plants terrestrial, epipetric, or epiphytic; rhizome creeping, green to blackish, with two rows of alternately arranged petioles on the dorsal surface, scaly near the apex; rhizome stele dorsiventral, composed of two unequal meristeles connected by lateral strands, the ventral meristele wider and the dorsal one narrower, bearing roots from either the ventral, dorsal, or connecting meristeles; petiole terete, scaly at base, glabrous distally, greenish to atropurpureous, the base swollen and often persisting after the leaf has fallen and decayed; lamina usually 1-pinnate or (in *A. cardiophyllum*) simple and cordate; rachis not or very shallowly grooved, with or without perpendicular or flat green wings, lacking buds; costae bordered by a flange of green

TABLE 1. The Eigen vector values for each PC in the analyses of *A. delitescens*, *A. hoffmannii*, *A. laetum*, *A. ortegae*, and *A. purpurascens* (Fig. 4).

Character (Fig. 3)	Principal component			
	1	2	3	4
LL	0.579	−0.699	0.200	0.043
PL	0.896	−0.233	0.086	0.064
PW	0.833	−0.151	0.110	−0.055
NP	−0.112	−0.811	0.388	0.172
PNL	0.936	0.032	−0.045	−0.143
PBL	0.579	−0.531	−0.393	0.072
PML	0.912	0.098	−0.237	−0.030
PEL	−0.044	−0.720	−0.497	−0.163
NV	0.796	0.432	0.170	0.077
DPB	0.263	0.165	−0.370	0.696
OD	−0.157	−0.304	0.395	0.157
TD	−0.245	0.306	−0.617	0.128
NS	0.737	0.093	0.018	0.428
SL	0.667	−0.028	−0.098	−0.129
DE	0.272	0.130	−0.225	−0.469
DC	0.058	−0.542	−0.614	−0.113
SGL	0.732	−0.092	−0.101	−0.336
SGW	0.838	0.241	−0.096	−0.018
NL	0.757	0.403	0.074	−0.176
RW	0.483	−0.435	0.274	0.054
PBW	0.752	−0.159	0.051	0.161
DBP	0.614	0.172	−0.075	0.481
RT	0.782	0.223	0.279	−0.303

TABLE 2. The Eigen vector values for each principal component in the analyses of *A. obtusifolium*, *A. repandulum*, *A. riparium*, *A. volubile*, and *A. triquetrum* (Fig. 5).

Character (Fig. 3)	Principal component	
	1	2
LL	0.866	−0.343
PL	0.721	0.337
PW	0.646	0.218
NP	0.696	−0.561
PNL	0.887	0.089
PBL	0.649	0.291
PML	0.659	0.452
PEL	0.010	0.722
DPB	−0.602	0.491
OD	0.511	−0.355
TD	−0.392	0.560
NS	0.798	−0.214
SL	0.599	0.309
DE	0.476	0.413
DC	0.024	0.523
SGL	0.489	0.363
SGW	0.314	0.590
RW	0.645	0.089
PBW	0.770	−0.041
DBP	0.264	−0.702

tissue that is decurrent on the adaxial surface of the rachis; decurrent margins of the pinnae not thickened; veins free or (in *A. cardiophyllum*) anastomosing; spores bilateral, ellipsoid to subglobose, the perispore commonly cristate, but occasionally spiny or papillose; $x = 38$ or 39.

1. Asplenium delitescens (Maxon) L. D. Gómez, Brenesia 8: 52. 1976. *Diplazium delitescens* Maxon, Contr. U.S. Natl. Herb. 10: 497, t. 56, fig. 1. 1908. TYPE: Cuba. Oriente: vic. of San Luis, 18 Feb. 1902, *Pollard & Palmer 348* (holotype, US; isotypes, F, MO). Figure 6A; Map 2.

Plants terrestrial; roots 1–1.5 mm wide; rhizome 3.5–7 mm wide, nearly naked; scales 2–2.5 mm × 0.25–0.35 mm, black-brown, narrowly lanceolate, toothed; petiole bases 2.8–4.5 mm wide, swollen, 1–2 mm distant from each other on the same row; petiole 15–25 × 0.15–0.2 cm, ca. ½ the

KEY TO THE NEOTROPICAL SPECIES OF *ASPLENIUM* SECT. *HYMENASPLENIUM*

1a. Leaf apex conform, subconform, or hastate; spores spiny or papillose; rhizome greenish when living (sometimes turning blackish upon drying).
  2a. Pinna apices obtuse or rarely acute; pinna pairs 3–10, usually with a free basal acroscopic lobe; spores papillose; plants rheophytic, usually under or near waterfalls; Costa Rica, Panama, Colombia, Venezuela, Antilles ..... 4. *A. obtusifolium* L.
  2b. Pinna apices acute or rarely obtuse; pinna pairs 8–18, usually without a free basal acroscopic lobe; spores spiny; plants epiphytic or epilithic and (usually) on rocks along streams.
    3a. Rachis strongly carinate abaxially, triangular in cross section, with adaxial green wings in the same plane as the lamina (these wings are difficult to distinguish in dried material); Ecuador, Peru, Bolivia, Paraguay, southern Brazil.
      4a. Plants epilithic; petiole ca. ½ as long as the lamina length; Bolivia, Paraguay, southern Brazil ..... 9. *A. triquetrum* Murakami & R. C. Moran
      4b. Plants epiphytic; petiole ¼–½ as long as the lamina; Amazonian Ecuador and Peru ..... 7. *A. repandulum* Kunze
    3b. Rachis rounded abaxially, terete or semi-terete in cross section, with adaxial green wings perpen-

dicular to the plane of the lamina (the wings difficult to see in dried specimens); southern Mexico to western Venezuela and Ecuador.

5a. Petioles ¼–½ as long as the lamina; plants twining around small trees or saplings; rhizome internodes 1–2.5 cm long; Costa Rica, Panama, western Colombia, western Ecuador ..... 10. *A. volubile* Murakami & R. C. Moran

5b. Petioles ½ to equaling the lamina; plants usually on boulders along streams; rhizome internodes 0.2–0.6 cm long; Mexico to western Venezuela and Ecuador ..... 8. *A. riparium* Liebm.

1b. Leaf apex nonconform, pinnatifid; spores cristate; rhizome brown or blackish when living.

6a. Free pinna pairs 2–6(–8); rachis green; Mexico to Panama, Trinidad, Venezuela, Colombia ..... 2. *A. hoffmannii* Hieron.

6b. Free pinna pairs 6–25; rachis atropurpureous to castaneous.

7a. Veins (in the middle of the pinnae) 2–4-forked; rachis grooved, with an adaxial green wing perpendicular to the plane of the lamina; western Venezuela, and Ecuador and Peru on the eastern side of the Andes ..... 5. *A. ortegae* Murakami & R. C. Moran

7b. Veins (in the middle of the pinnae) 1–2-forked; rachis grooved but without adaxial green wings.

8a. Pinnae pinnatifid throughout their length, usually lobed ¼–½ to the costae; Ecuador ..... 6. *A. purpurascens* Mett. ex Kuhn

8b. Pinnae entire to serrate, sometimes with a basal auricle on the acroscopic side and/or basiscopic side.

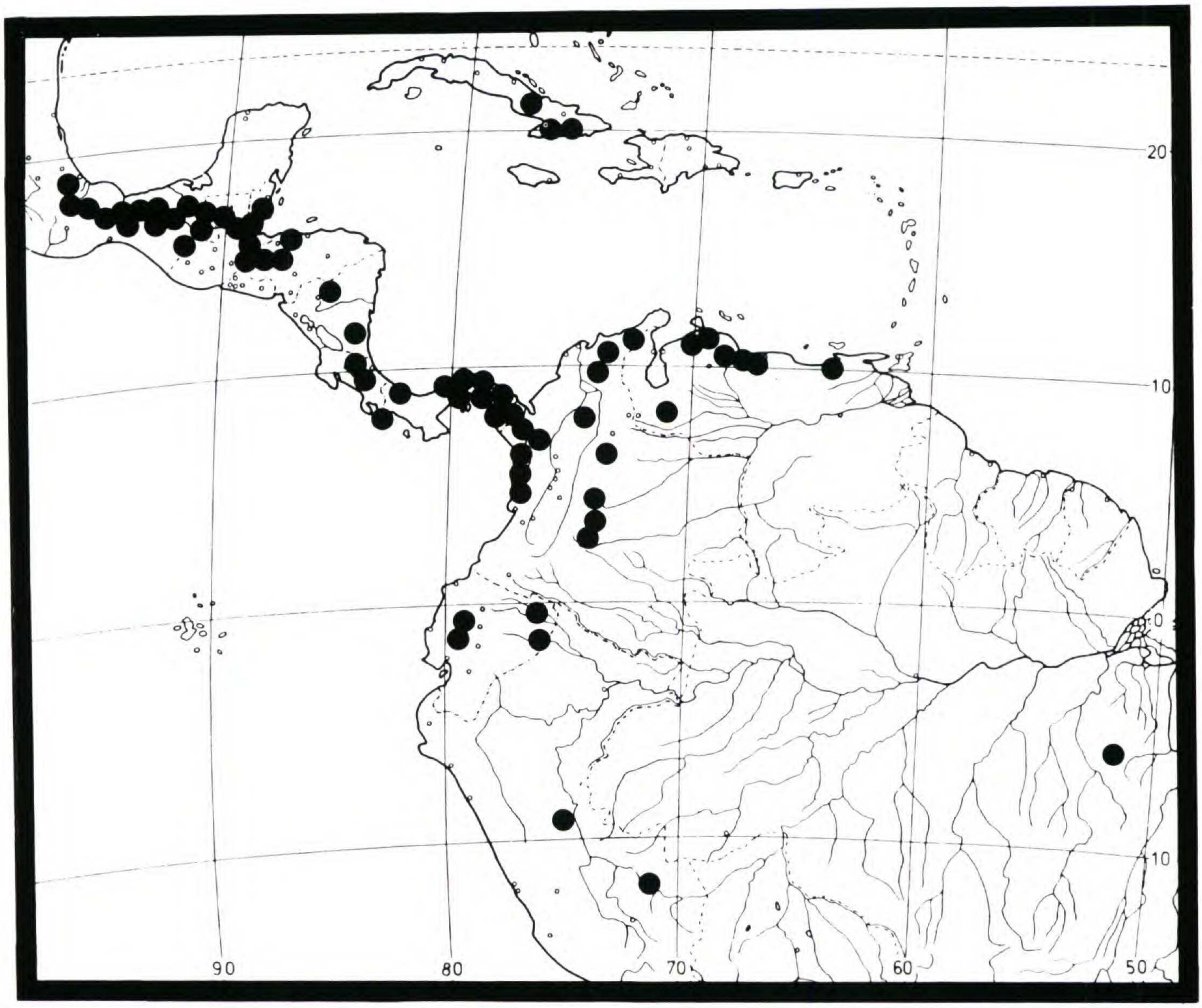
9a. Pinnae 7–11 × 1.2–2 cm, 6–9 pairs; petiole and rachis stramineous to greenish brown; southern Mexico to Venezuela and Peru, Cuba ..... 1. *A. delitescens* (Maxon) L. D. Gómez

9b. Pinnae 2–6 × 0.6–1.2 cm, 10–25 pairs; petiole and rachis atropurpureous; Mexico to southern Brazil ..... 3. *A. laetum* Sw.

leaf length, stramineous to green-brown, occasionally partly purplish, glabrous; lamina 20–30 cm long, green, 1-pinnate, deltate with an abruptly reduced, pinnatifid apex; rachis like the petiole, grooved and with herbaceous green wings; lateral pinnae 7–11 × 1.2–2 cm in the middle of the leaf, 6–9 pairs, lanceolate to linear-lanceolate, long-acuminate, the margin slightly toothed, the teeth 0.5–1 mm deep, excavate on the basal basiscopic side ⅙–¼ of the total length, acroscopic base truncate, auricle 1–4 mm long; veins 2-forked; sori 5–10 mm long, occasionally diplazioid in the abruptly reduced pinnae near the apex; spores 33–38 μm long, 64 per sporangium, perispore cristate.

Additional specimens examined. MEXICO. CHIAPAS: Mpio. de Ocosingo, ruins of Yaxchilán on the banks of the Río Usumacinta, 300 m, *Breedlove 29935* (F, MO, NY); Mpio. de Las Margaritas, W side of Laguna Miramar E of San Quintin, 350 m, *Breedlove 33123* (F, MICH, NY); Mpio. of Las Margaritas, low ridges at the confluence of the Río Ixcan with the Río Lacantum (Río Jatate) on the Guatemala border, 300 m, *Breedlove & McClintock 34140* (MO); Palenque, in rocky streamside forest by the ruins, 170 m, *Chater et al. 128* (BM, MO); Mpio. Ocosingo, 3 km S de Frontera Corozal, sobre la orilla del Río Usumacinta, 120 m, *Martínez S. 8008* (MO); Mpio. Ocosingo, en la zona Marquez de Comillas, a 6 km SE de Ejido Benemérito de las Americas, con rumbo a Flor de Cacao, 160 m, *Martínez S. 8136* (MO, NY); 24 km al SE de Crucero Corozal, camino Palenque–Boca Lacantum, 200 m, *Martínez S. 8402* (MO); Mpio. Ocosingo, 16 km NW de Boca Lacantum a Palenque, 220 m, *Martínez S. 16399* (MO); Cerro de Macuspana, *Rovirosa 1038* (GH), *3135* (MO); Ruina Palenque, 100 m, *Saiki M234* (F, Z). OAXACA: Mpio. Sta. María Chimalapa, a pie de la Piedra Siniguichi en la cabecera del arroyo Huahuagtza, cerca de Piedra Blanca, 7 km E de Sta. María, 270 m, 16°55′N, 94°37′W, *Hernández G. 734* (MO, NY); filo del cerro al E del Arroyo Monte Rico, ca. 20 km al E de Sta. María, 400–500 m, 16°55′N, 94°42′W, *Hernández G. 1574* (MO, NY); ca. 25 km al E de Sta. María, cerro al N de la unión del Río Blanco (del S.) con el Río del Corte, al N del Río del Corte, 400–500 m, 16°55′N, 94°42′W, *Hernández G. 1920* (NY); ca. de 18 km NE de Sta. María por la vereda al Río Pinal, Chimalapilla, 300 m, 16°57′N, 94°36′W, *Hernández G. & González L. 1787* (MO); Dtto. Tuxtepec, 9 km S of Tuxtepec and 4 km W of Rte. 175, behind Fabricas de Papel Tuxtepec, 100 m, *Mickel 5784* (NY, UC); between Tuxtepec and Playa Vicente, 28 km SE of Rte. 147, 100 m, *Mickel 7212* (NY, UC); Dtto. Juchitán, 1 km N of Palomares, 1 km E of highway on road to La Pedrera "Paso de Buques," 100 m, *Mickel & Pardue 6843* (NY, UC); 5 km S of Palomares, 150 m, *Mickel & Pardue 6866* (NY). TABASCO: Teapa, 4 km SE of Teapa on road to Tacotalpa, base of Cerro de Madrugal, 300 m, *Croat 47908* (CR, MO). VERACRUZ: Córdoba, *Finck 159* (UC); Mpio. Hidalgotitlán, near Campamento La Laguna, 100 m, 17°17′N, 94°30′W, *Nee 29974* (F); Mpio. Hidalgotitlán, entre Hermanos Cedillo y La Escuadra, Río Solosúchil, 150 m, *Vásquez 977* (NY); 2 km al N del Poblado no. 2, zona de Uxpanapa, Mpio. Jesús Carranza, 100 m, *Vásquez T. 2485* (NY). BELIZE. STANN CREEK: Stann Creek railway, 17 mi., *Gentle 2714* (F, GH, MICH, NY); caves and railway, 33 m, *Schipp 8-275* (B). TOLEDO: Columbia Forest Reserve, ca. 1–2 mi. N of entrance, *Croat 24173* (MO); Condemn Branch Hills, *Gentle 5139* (GH, MO, S); in cohune ridge, Chavarrias road, Resemederes, across Columbia River, *Gentle 6261* (F, G, NY, S, UC). GUATEMALA. PROV. UNKNOWN: Los Amates, 30 m, *Deam 470* (GH), *Smith 5675* (NY). PETEN: ca. 4 km S of Lacandón, *Contreras 3432* (MICH, S); Chinchilá, Sebol Road, *Contreras 10500* (F); along Río San Diego, between Finca Yalpemech and San Diego, 50–150 m, *Steyermark 45308* (F). HONDURAS. ATLANTIDA: Lancetilla Valley, near Tela, 20–600 m, *Standley 54153* (F). COPAN:

FIGURE 6.—A. *Asplenium delitescens*, Panama, *Seibert 583* (MO).—B. Possible hybrid between *A. delitescens* ×*laetum*, Ecuador, *Luteyn et al. 8502* (NY).



MAP 2. The distribution of *Asplenium delitescens*.

20 km NW de Santa Rosa de Copán, hacienda Ocoteseco, 1,300 m, *Morales R. 65* (MO); Fort of La Cumbre, near creek, *Thieme 4* (UC); SANTA BARBARA: San Pedro Sula, 200 m, *Thieme 5675* (B, MO). NICARAGUA. MATAGALPA: El Carmen, carretera El Tuma a Waslala, 600–700 m, 13°13′N, 85°37′W, *Moreno 19063* (MO). ZELAYA: Dept. Bluefields, 3.6 km SE Cerro San Isidro, 65 m, 12°05′N, 83°45′W, *Proctor et al. 27114* (F). COSTA RICA. ALAJUELA: Aguacate, *Hoffmann 759* (B). SAN JOSE: Carrillo, 300 m, *Wercklé 17432* (B). PUNTARENAS: Palmar Norte, *Grayum et al. 9152* (MO, UC). PANAMA. BOCAS DEL TORO: vic. of Laguna de Chiriquí, *Hart 42* (UC). CANAL AREA: near Madden Dam, *Alston 8868* (BM); Barro Colorado Island, *Aviles 16* (F, MO); hill at Canal Zone boundary, vic. of Juan Mina, *Bartlett & Lasser 16580* (GH, MICH, MO); no locality, *Cornman 5121* (MICH); Colón to Empire, Panama Railroad, *Crawford 554* (BM, NY); Barro Colorado Island, Creek no. 8 S from Shannon Trail, growing in stream bed, *Croat 5192* (MO); Lutz Creek bank, *Croat 6516* (MO); Barro Colorado Island, Wheeler Trail 13, *Croat 8053* (MO); short cut to Lutz Trail behind animal house, *Croat 8515* (F, MO); Nemesia Trail 200, *Croat 8597* (MO); Armour Trail 2170, *Croat 8643* (F, MO); Barro Colorado Island, Armour Trail 850, *Croat 9425* (MO); Barro Colorado Island, Armour Trail 1040, *Croat 11639* (MO, NY); Barro Colorado Island, Drayton Trail 100, *Croat 12662* (MO); Barro Colorado Island, Armour Trail 500, *Croat 14056* (MO); vic. of Madden Lake along Boy Scout road, 100 m, *Croat 38327* (MO); Río Providencia 3 km SE of Achiote near W border of Canal Zone, 5–100 m, *Gentry 8679* (AAU, MO); *Hunnewell 16375* (MICH); Pipeline road, Limbo Hunt Club, *Kennedy & Andrews 1876* (MO); Barro Colorado Island, *Kenoyer 29* (GH); Valley of Masambí, on the road to Las Cascadas Plantation, 20–100 m, *Maxon 4677* (BM, GH, NY); Barro Colorado Island, Lake Gatún, *Maxon et al. 6807* (GH); trail along Río Petipie from road to Fort Sherman from Gatún Locks, *Mori & Kallunki 2672* (MO); 6 km E of Gamboa, headwaters of Río Casaya, *Nee 9026* (UC); Madden Dam, near Río Chagres, 50–75 m, *Seibert 583* (GH, MO); 4 mi. NE of Gamboa, vic. of Gold Creek, *Seibert 587* (F, MO); Barro Colorado Island, *Shattuck 189* (F, MO); Allison Armour trail, *Wetmore & Woodworth 105* (GH); Madden Lake, *Witherspoon & Witherspoon 8797* (MO). CHIRIQUI: Burica Peninsula, 8 mi. W of Puerto Armuelles, 200 m, *Croat 22493* (F, MO). COLON: ca. 6 km N of Chilibre, along shores of Madden Lake, 25–50 m, 9°12′N, 79°36′W, *Knapp 2716* (MO). DARIEN: near the mouth of Río Yape, 20 m, *Allen 347* (MO); Río Chico, from Yavisa at junction with Río

Chucunaque to ca. 1 hour by outboard from junction, *Burch et al. 1095* (MO); E slope of Cerro Sapo, 500 m, *Hammel 1266* (MO); Paya to Pucra, *Stern et al. 235* (F, GH, MO); vic. of Campamento Buena Vista, Río Chucunaque above confluence with Río Turquesa, *Stern et al. 824* (MO), *Tyson et al. 4835* (MO); 2 mi. E of Santa Fé, *Tyson et al. 4835* (UC); 2 km E of Juan Díaz, *Cornman 512* (MICH, MO, UC); Piriati, S of Pan American Hwy., 200–400 m, 9°00′N, 78°30′W, *Hamilton 529* (MO, UC); 1859–1861, *Hayes 57* (BM, F, GH); Bajia Sta., *Hayes 355* (BM, K); Juan Díaz, Topia River, 50 m, *Killip 2708* (B, MICH, S), 50 m, *Killip 2806* (MO); Gatuncillo River, *Rowlee & Rowlee 415* (NY); Panama Viejo?, *Seemann 66* (BM); Marraganti and vic., 0–60 m, *Williams 1026* (NY). PANAMA: Campana Hill, 800 m, *Alston 8925* (BM); Isla de Bayano, trocha D, *Correa A. et al. 2973* (F, MO); near Juan Díaz, 0–75 m, *Killip 2512* (S); Serranía de Majé, ridges S of Chocó village of Ipeti, Río Ipeti drainage system, 500–600 m, 8°47′N, 78°27′W, *Knapp & Sytsma 2334* (AAU, CR, MO); Chilibre, *Martínez 9* (MO); Río Bayano a 5 km del Camp. de Majé, *Rivera 23* (CR); Río Tapia, *Standley 26184* (MO). CUBA. ORIENTE: Sierra de Nipe, ad cañon fluminis Canapú, *Ekman 2533* (G, NY, S); near Bayate, Cayo del Rey, *Ekman 2760* (S).VENEZUELA. ARAGUA: Colonia Tovar, *Fendler 143* (G, NY). BARINAS: along Río Caparo, 2–4 km up river from dam site, 100–200 m, 7°41′N, 71°28′W, *Liesner & González 9473* (MO). FALCON: Parque Nacional Quebrada el Toro, 600 m, *van der Werff 402* (UC). LARA: border area between Edo. Lara/Yaracuy, Sierra de Aroa, 10–13 mi. NW of Urachiche along dirt road leading NW from Urachiche to Duaca, 1,400 m, 10°14′N, 69°04′W, *Smith et al. 1340* (MO). SUCRE: Dtto. Sucre, along Quebrada el Tigre, S of Fila La Baqueta (in the future basin of Represa Neveri), 350 m, 10°07′N, 64°19′W, *Davidse & González 19242* (MO, NY, UC). TERRITORIO FEDERAL AMAZONAS: upper Orinoco region, Ugueto, *Croziat 794* (BR). COLOMBIA. ANTIOQUIA: Guapá, 53 km S of Turbo, 60 m, *Haught 4628* (COL); 53 km S of Turbo, Guapá, 80 m, *Haught 4684* (NY, S). BOLIVAR: Boca Verde, on Río Sinu, 100–300 m, *Pennell 4213* (GH); 12 km S of Carraipia, Com. Guajira, 450 m, *Haught 4286* (COL, NY). CHOCO: near Caserío La Teresita, 0.5–2.5 km N of the INDERENA camp on the Río Truando, 50–100 m, *Lellinger & de la Sota 532* (COL); Nercua and Divide, *Schott 57* (F); Parque Nacional Natural Los Katíos, sector Cacarica, *Zuluaga R. 986* (COL). MAGDALENA: ca. 6 km E of La Jagua, Sororia Creek, 200 m, *Haught 3613* (COL); Santa Marta, *H. H. Smith 2693* (NY). SANTANDER: vic. of Puerto Berrio, between Carare and Magdalena rivers, 100–700 m, *Haught 1715* (COL, GH); SE of Puerto Berrio, 100 m, *Haught 2865* (COL, GH, UC). ECUADOR. LOS RIOS: Canton Vinces, Jauneche Forest, between Mocachi and Palenque, on Estero Peñafiel, 70 m, *Dodson et al. 7089* (AAU, MO, QCNE). MANABI: on road from Quevedo to Calceta, Hacienda Aurora, 400 m, *Haught 2976* (GH, S, UC). PERU. HUANUCO: Tingo María, on steep rocky slope above Río Huallaga, 650 m, *Croat 21075* (MO); along road from Tingo María to Monzón, vic. of Río Patay Rondos, Cuevas de Gucharo "Parque Nacional Tingo María," 650 m, *Croat 57945* (MO); hills above river on steep limestone forested slope, *Moran 3676* (MO); Pachitea, Dtto. Puerto Inca, Bosque Nacional de Iparía, 400–500 m, *Schunke V. 2967* (F). BRAZIL. PARA: Serra dos Carajás, ca. 6 km NW of AMZA camp 3-Alfa, on the road to camp 4-Alfa, 200–250 m, 5°47′S, 50°34′W, *Sperling et al. 6035* (GH, NY, UC); 12 km W of camp ECB on the ferrovia, ca. 57 km W of road BR 150, 150 m, 5°35′S, 49°15′W, *Sperling et al. 6381* (BM, F, GH, NY).

Asplenium delitescens occurs from Mexico to Peru and east-central Brazil, and Cuba (Map 2). It grows terrestrially in wet forests from 0 to 800(–1,400) m. Rarely, it grows on rocks.

The species is characterized by stramineous or greenish petioles, few (6–9) pinna pairs, and deltate laminae with abruptly reduced apices (Fig. 6A). Where the lamina abruptly contracts to the narrowed apical segment, the pinnae and lobes are often retuse. Occasional specimens are intermediate between *A. delitescens* and *A. laetum* (Fig. 6B). These are treated in the hybrid section of this monograph.

Asplenium delitescens closely resembles *A. abscissum* Willd. (which is not a member of section *Hymenasplenium*) in leaf cutting and outline. To the naked eye, *A. abscissum* differs from *A. delitescens* by its erect (rather than creeping) rhizome and the obovate, evenly serrate (rather than quadrangular-truncate, and irregularly serrate) pinnae that are immediately beneath the apical segment. Two microscopic characters also distinguish the species. Both species are sparsely scaly abaxially where the pinnae join the rachis. In *A. abscissum*, the scales are 0.2–0.6 mm long, reddish, and uniseriate. In *A. delitescens*, the scales are 0.5–1.5 mm long, blackish, and uni- to triseriate. The structure of the pinna and rachis is also diagnostic. *Asplenium abscissum* has a slightly raised costa and a thickened pinna margin decurrent on the side of the rachis (Fig. 16C). In contrast, *A. delitescens* has a slightly sunken costa bordered by a green flange of tissue that is decurrent on the adaxial surface of the rachis (Fig. 16D). The decurrent margin of the pinna is not thickened (this form of the rachis and costa juncture is constant throughout section *Hymenasplenium*).

Smith (1976) first pointed out that *A. delitescens* and several other neotropical *Asplenia* belonged to section *Hymenasplenium*. He also realized that this species belonged to *Asplenium*, rather than *Diplazium* where it was originally placed, and gave an excellent discussion on the characteristics that distinguish the two genera.

2. Asplenium hoffmannii Hieron., Hedwigia 60: 258. 1919. TYPE: Costa Rica. Alajuela: Aguacate, Aug. 1857, *Hoffmann 836* (holo-

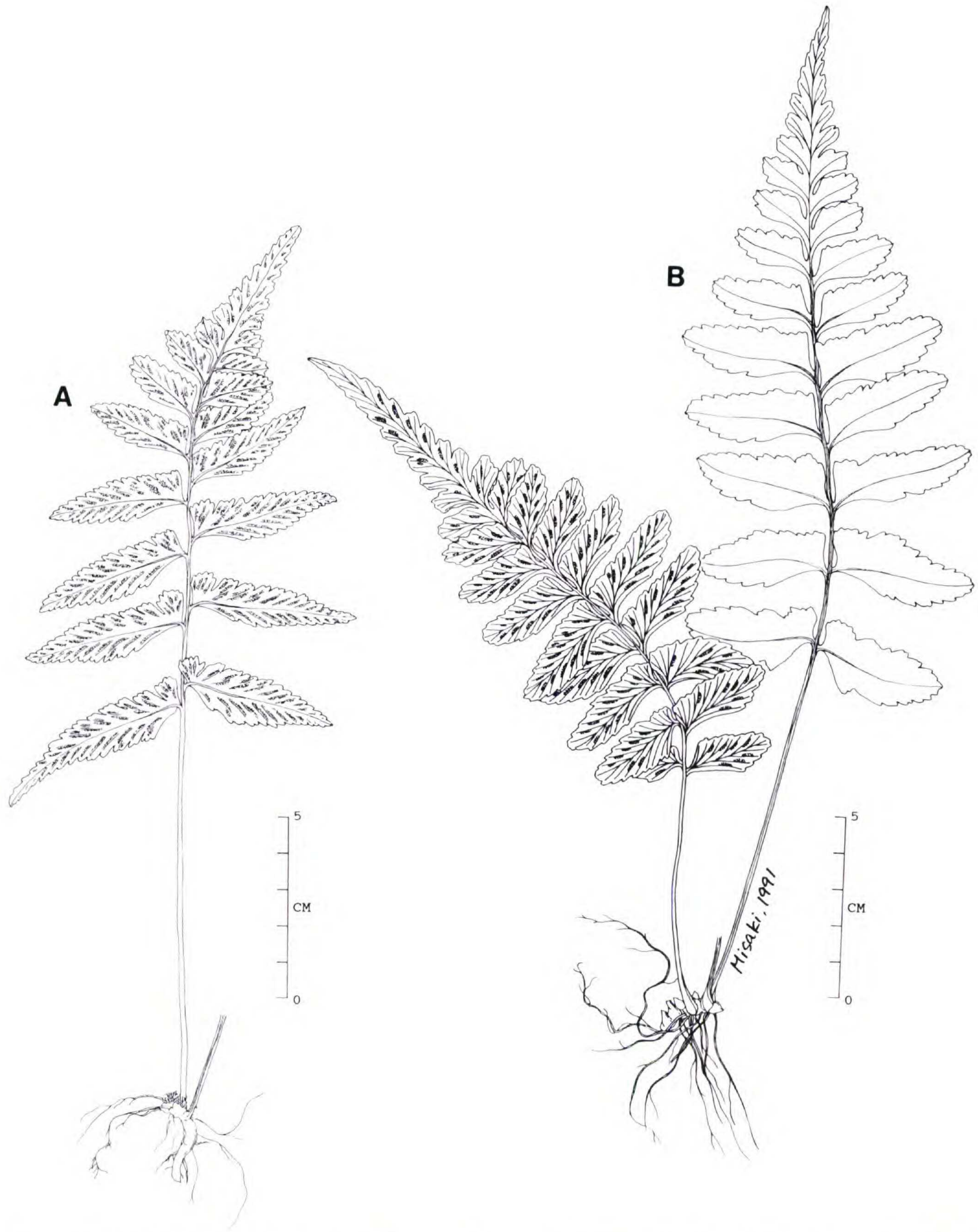
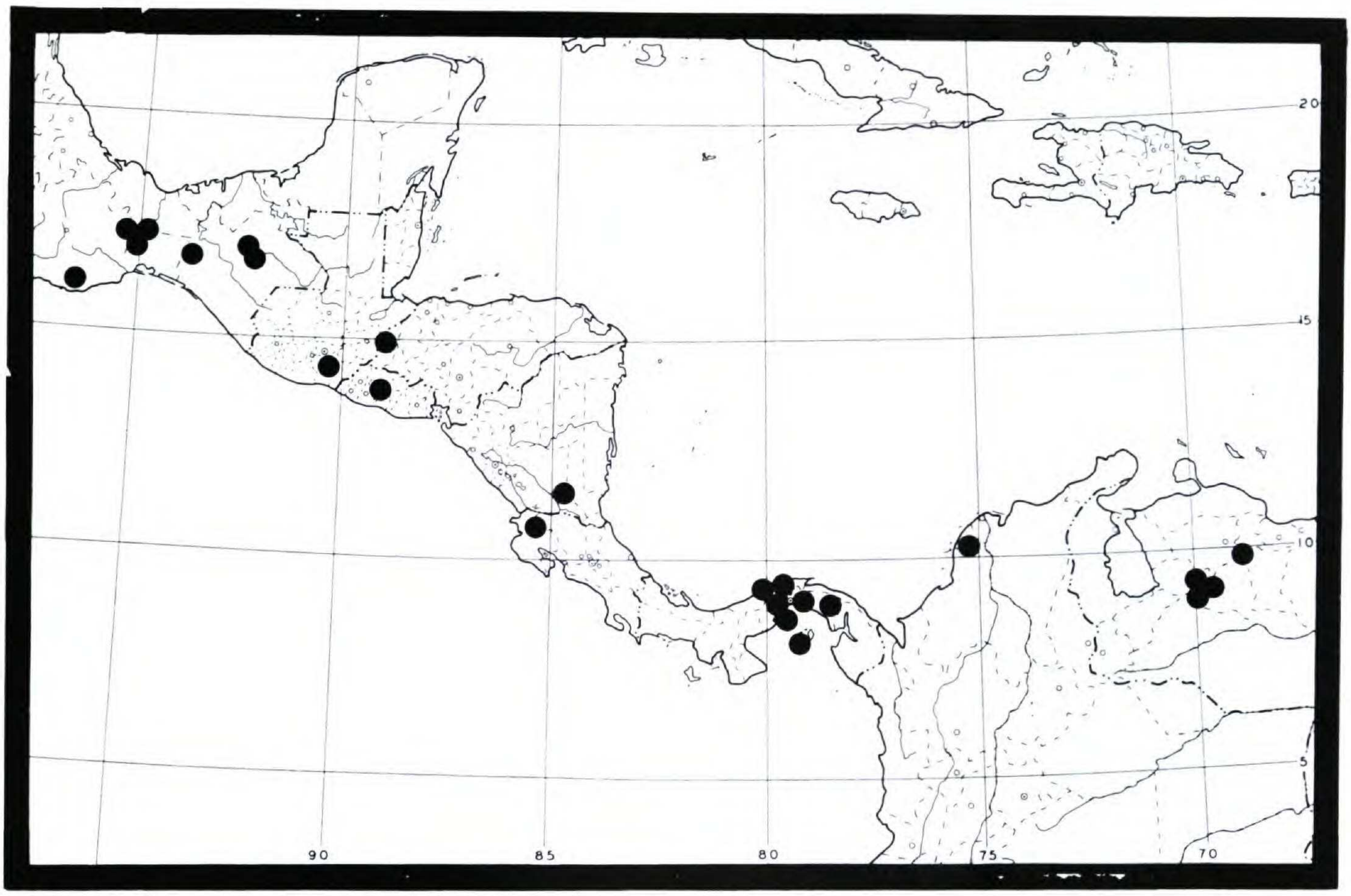


FIGURE 7. *Asplenium hoffmannii.*—A. Panama, *Johnston 131* (US).—B. Mexico, *Breedlove 33893* (MO).

type, B; isotype, NY fragment, photo BM ex B). Figure 7; Map 3.

Asplenium membranifolium Maxon, Amer. Fern J. 24: 72. 1934. TYPE: Panama. Panamá: ca. 10 mi. E of Panama City, *Killip 2567* (holotype, US; isotype, NY fragment).

Plants epilithic, rarely terrestrial; roots 0.4–0.6 mm wide; rhizome 1.8–3.5 mm wide, almost naked; scales 0.8–1.3 × 0.2–0.3 mm, black-brown, ovate-lanceolate; petiole base 1.4–2.4 mm wide, swollen, 0.3–2.7 mm distant from each other on the same row; petiole 4–9 × 0.05–0.1 cm, ¼–½ the leaf length, greenish, glabrous; lamina 15–40 cm long, light green, membranaceous, 1-pinnate,



MAP 3. The distribution of *Asplenium hoffmannii*.

lanceolate to oblong with attenuate apex; rachis green, grooved, with perpendicular wings; lateral pinnae 2–3.5 × 0.7–1.1 cm in the middle of the leaf, 2–6(–8) pairs, subquadrangular to lanceolate, the margin deeply toothed, 1–2 mm deep, excavate for ca. ½ the length of the basiscopic side, obtuse to acute at apex, shortly stalked at lower pinnae, auricle absent; veins 1–2-forked; sori 3–5 mm long; spores 33–38 μm, 64 per sporangium, perispore cristate.

Additional specimens examined. MEXICO. CHIAPAS: Mpio. of Ocosingo, ruins of Yaxchilán on the banks of the Río Usumacinta, 300 m, *Breedlove 33893* (MO); ruins of Yaxchilán on banks of the Río Usumacinta, 300 m, *Breedlove 42851* (MO); Tuxtla–San Andrés, *Schmid s.n.* (Z). OAXACA: Mpio. Sta. María Chimalapa, ca. 5 km N de Sta. María, Arroyo Mactaspac, cerca del Río del Corte, 200 m, 16°56′N, 94°41′W, *Hernández G. 2021* (NY); Dtto. Pochutla, 29.6 km NE of Pochutla, Oaxaca–Pochutla road, 300 m, *Mickel 1304* (NY); Dtto. Juchitán, 10–15 km W of Rte. 185, road from near Palomares toward Tuxtepec, 100 m, *Mickel 7411* (NY, UC); Dtto. Pochutla, 15 km N of Pochutla, 300 m, *Mickel & Leonard 5138* (NY); Juquila, 34 km N of Puerto Escondido, 500 m, *Mickel 6077* (NY). GUATEMALA. SANTA ROSA: near Oratorio, 1,200 m, *Standley 60656* (F). HONDURAS. COPAN: Ruinas de Copán, *Bernoulli 834* (B), *Bernoulli & Cario 290* (B, K). EL SALVADOR. PROV. UNKNOWN: El Salto near Huizuca, Río Las Lajas, 300 m, *Seiler 718* (NY). NICARAGUA. RIO SAN JUAN: San Bartolo, *Seymour 6200* (MO). COSTA RICA. GUANACASTE: 4 km W Bagaces, *Opler s.n.* (CR). GUANACASTE: Rincón de la Vieja National Park, slopes of Volcán Santa María, 700–900 m, 10°46′N, 85°18′W, *A. R. Smith et al. 1961* (CR, MO, UC). PUNTARENAS: Palmar Norte, *Grayum et al. 9159* (MO, UC). PANAMA. CANAL AREA: Juan Mina, Flat Rock, Chagres River, *Bartlett & Lasser 16843* (GH, MICH, MO); Alajuela, *Cornman 548* (MICH, UC); Fort Sherman, *Dwyer 6823* (MO); trail along Río Petitpie, from road to Fort Sherman from Gatun Locks, *Mori & Kallunki 2670* (MO); near Gatú, hills W of the Canal, *Standley 27218* (L, MICH, NY, UC); 1 mi. N of Summit Garden, on rock embankment of bridge just above small creek, *Sytsma 2314* (MO); Old Fort San Lorenzo, from rocks near fort in shade, 10 m, *Tyson 2237* (MO); Madden Forest Preserve, across from George W. Green Park, *Welch 19856* (MO); vic. of Salamanca Hydrographic Station, Río Pequení, 80 m, *Woodson et al. 1601* (GH, MO). COLON: ca. 6 km N of Chilibre, along shores of Madden Lake (Lago Alajuela), 25–50 m, 9°12′N, 79°36′W, *Knapp 2686* (MO); Panamá Viejo, *Seemann 72* (BM; photos GH, UC); Taboga Island, *Cornman 597* (MICH, UC); San José Island, Perlas archipelago, ca. 55 mi. SSE of Balboa, *Johnston 131* (BM, GH, U), *258* (BM, GH), *385* (BM, GH); ca. 55 mi. SSE of Balboa, *Johnston 444* (GH); Panamá Viejo, *Seemann 369* (BM). PANAMA: Madden Dam, forest near spillway, at bottom of dam, 50 m, 9°13′N, 79°37′W, *Churchill 3851* (MO, UC); 5 mi. W of bridge over Bayano Lake, 200 m, *Hammel & D'Arcy 5106* (MO); Río Tecumen, *Standley 29372* (GH). TRINIDAD: Blue Basin, *Hombersley 257* (BM). VENEZUELA. ARAGUA: prope coloniam Tovar, *Fendler 61, pro parte* (NY, mixed with *Asplenium* ×*incisoserratum*).

PORTUGUESA: Dtto. Araure, Los Hijitos, entre Agua Blanca y San Rafael, 160 m, *Ortega & Aymard 2089* (UC); Dtto. Guanare, near Desembocadero, 400 m, *A. R. Smith et al. 856* (MO, UC); Dtto. Guanare, along road to San José de La Montaña, 500 m, 9°20′N, 69°43′W, *A. R. Smith et al. 1095* (NY, UC); NE de Boca de Monte, 28–32 km NNE de Guanare, arriba del puente sobre el Río María, 400–500 m, 9°18–19′N, 69°42–43′W, *Steyermark et al. 127064* (MO, UC); 7 km NE de Boca de Monte, 22 km NE del vado del Río Suruguapo, 45 km NE por la autopista Guanare–Ospino, en el sitio Las Marías, E de Guanare, 400 m, 9°19′N, 69°41′30″W, *Steyermark et al. 127236* (MO, UC). COLOMBIA. BOLIVAR: Torrecilla, near Turbaco, 150–300 m, *Killip & Smith 14658* (K, NY).

Asplenium hoffmannii occurs from southern Mexico to Colombia, Venezuela, and Trinidad (Map 4). It grows on rocks along deeply shaded streams in wet forests. Rarely, it grows on old walls or terrestrially. The elevation ranges from 0 to 500(–900) m.

The species is characterized by membranaceous laminae, few (1–3) leaves per rhizome, deeply and evenly serrate pinnae, and few (usually 2–6) pinna pairs (Fig. 7). It hybridizes with *A. laetum* to produce *A.* ×*incisoserratum* (which see; Fig. 16). The hybrid differs from *A. hoffmannii* by having more pinna pairs (6–14), more than three leaves per rhizome, basally darkened petioles (especially in large leaves), and aborted spores.

3. Asplenium laetum Sw., Syn. Fil. 79, 271. 1806. NEOTYPE (designated by Proctor, 1985): Schkuhr, Krypt. Gew. 1: 65, t. 70. 1809. Figure 8A; Map 4.

Asplenium virens Desv., Mém. Soc. Linn. Paris 6: 273. 1827, not C. Presl, 1825. TYPE: "America," *collector unknown* (P-Herb. Desv.; photos GH, US ex P).

Asplenium schkuhrianum C. Presl, Tent. Pterid. 107. 1836, nom. superfl. for *A. laetum* Sw. LECTOTYPE (designated by Morton & Lellinger, 1966): Venezuela. Distrito Federal: Caracas, *Bredemeyer s.n.* (W-Herb. Jacquin). This is probably the specimen used by Schkuhr (1809) in drawing his t. 70, which has been designated as the neotype of *A. laetum* (see above).

Asplenium lugubre Liebm., Mexic. bregn. 243 (seors. 91). 1849. LECTOTYPE (designated by A. R. Smith, 1981): Mexico. Veracruz: Baranca de Mirador, *Liebmann* [Fl. Mex. 322] (lectotype, C not seen; isolectotypes, B, K).

Plants terrestrial or epilithic; roots 0.5–0.8 mm wide; rhizome 2.5–6.5 mm wide, sparsely scaly; scales 2–3.3 × 0.23–0.33 mm, black-brown, linear-attenuate; petiole base 1.5–3.5 mm wide, swollen, 0.4–2.5 mm distant from each other on the same row; petiole 4–20 × 0.09–0.15 cm, ⅕–½ the leaf length, blackish reddish purple, sometimes green, grooved, sparsely scaly at base; lamina 15–40 cm long, 1-pinnate, lanceolate to oblong with attenuate apex; rachis like petiole, grooved and with green, perpendicular, herbaceous wings; lateral pinnae 2–6 × 0.6–1.2 cm in the middle of the leaf, 10–25 pairs, subquadrangular, the margin slightly to strongly toothed, the teeth 0.5–2 mm deep, the basiscopic side excavate basally for ca. ½ the pinna length, the apex acute, the base broadly cuneate and almost sessile to stalked, auricle 0–3 mm long; veins 1-forked; sori 2.5–7.5 mm long; spores about 27–38 μm, 64 per sporangium, perispore cristate.

Additional specimens examined. MEXICO. CHIAPAS: on the Guatemala border, Mpio. of Las Margaritas, low ridges at the confluence of the Río Ixcan with the Río Lacantum (Río Jatate), 300 m, *Breedlove 34197* (MICH, MO); Mpio. of Frontera Comalapa, 6–8 km E of Frontera Comalapa along road to Ciudad Cuauhtémoc, 1,000 m, *Breedlove 39059* (NY); 13 km N of Berriozabal, Mpio. de Berriozabal, 1,000 m, *Breedlove & Smith 21683* (F, MICH, MO, NY); Mpio. of Cintalpa, SE of Cerro Baul on the border with Oaxaca, 16 km NW of Rizo de Oro along a logging road to Colonia Figaroa, 1,600 m, *Breedlove & A. R. Smith 31319* (NY); los alrededores de la zona Arquelógica de Palenque, *Cabrera et al. 1938* (BM, MO); Palenque, in forest by the ruins, 170 m, *Chater et al. 131* (BM, MO); 1864–1870, *Ghiesbreght 426* (K); Finca Mexiquito, *Purpus 6735* (F, MO, UC), *Purpus 6765* (UC); Finca Irlanda, *Purpus 7241* (UC); Ruina Palenque, 100 m, *Saiki M-230* (F, Z). OAXACA: Mpio. Sta. María Chimalapa, Arroyo Piedra de Tigre, ca. 8 km al O de Sta. María, 220 m, 16°53′N, 94°43′W, *Hernández G. 1008* (NY); Chimalapilla, ca. de 18 km al NE de Sta. María por la vereda al Río Pinal, 300 m, 16°57′N, 94°36′W, *Hernández G. & González 1787* (NY); Dtto. Tuxtepec, 4–9 km S of Valle Nacional on Rte. 175, 200–700 m, *Mickel 5881* (NY, UC); Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, trail E of Rte. 175 at Campamento Vista Hermosa toward Ladu, 500–650 m, *Mickel 6461* (NY, UC); Dtto. Ixtlán, 76 km N of Ixtlán de Juárez on Rte. 175, 5 km S of Vista Hermosa, Campamento La Esperanza, *Mickel 7188* (NY, UC); vic. of Cafetal Concordia, 400–650 m, *Morton & Makrinius 238* (F); Tuxtepec, above Jalapa de Díaz, 330 m, *Hallberg 1468* (NY), 400 m, *Hallberg 1471* (NY). TABASCO: cerro arriba del Ejido Zunu, Mpio. Tacotalpa, Ejido Zunu en el camino de la Est. Tacotalpa hacia Tapijulapa, 180 m, *Cowan & Magana 3139* (MO, NY); Tacotalpa, 3 km al E del ejido Lázaro Cárdenas, 50 m, *Cowan 2072* (NY); Teapa, 3 km E of Teapa, slope of Cerro las Campanas, ca. 50 km S of Villahermosa, 50–100 m, *Conrad et al. 2889* (MO); Cerro de Cocorrá, near Teapa, *Rovirosa 828* (NY). VERACRUZ: près Córdova, Chiquihuite, *Bourgeau 2151* (K, L, MO, NY); Mpio. Hidalgotitlán, 6 km E de Cedillo camino a La Laguna, 110 m, *Dorantes et al. 2555* (F, UC); Orizaba, 1855 m, *Müller 1835* (NY); in Dec. 1921, *Purpus 174* (Z); Mirador, Barranca de San Francisco, 1,000 m, *Ross 688* (BM). BELIZE. STANN CREEK: caves and railway, 30 m, *Schipp*

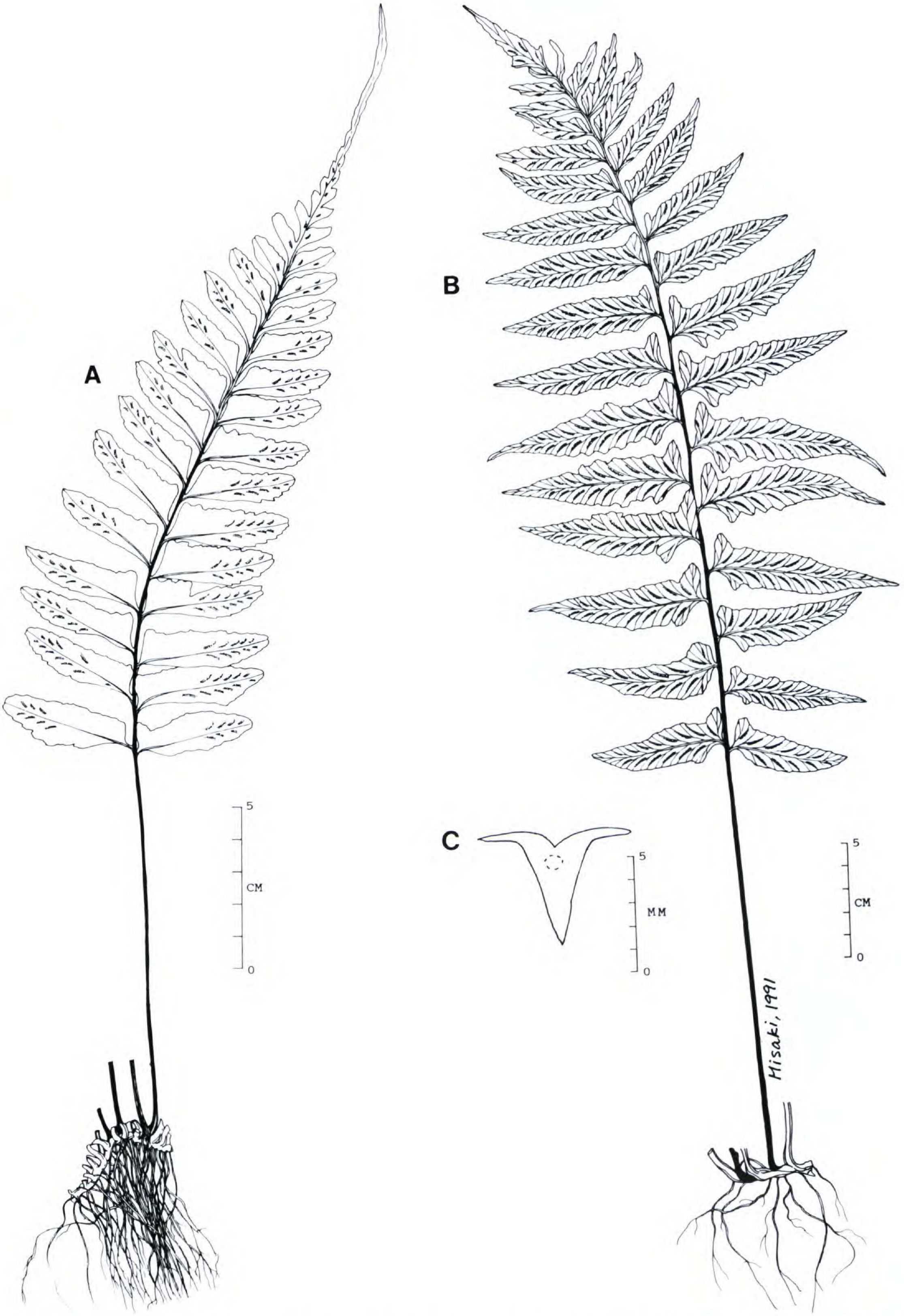
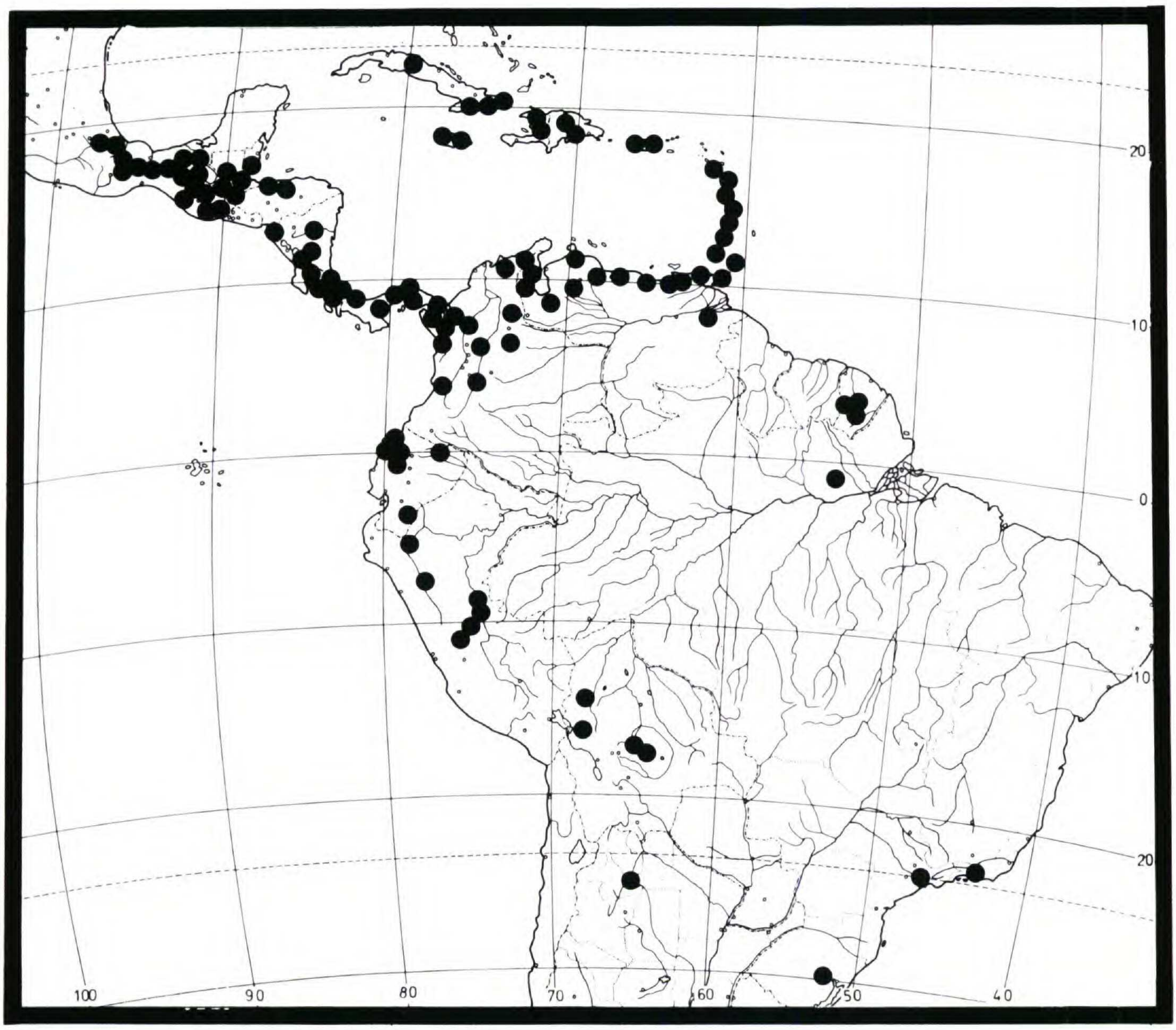


FIGURE 8.—A. *Asplenium laetum*, Panama, *Mori & Kallunki 2826* (MO).—B, C. *Asplenium triquetrum*, Brazil, *Dusén 6774* (MO). Cross section of rachis shown in C.



MAP 4. The distribution of *Asplenium laetum*.

S-277 (B). TOLEDO: Edwards road beyond Colombia, on hilltop beyond Central camp, *Gentle 7378* (BM, F, G, MICH, NY, S, UC); Colombia Forest Reserve, vic. of forest camp ca. 6 mi. S of Cabro, in upper Río Grande drainage area, 300 m, *Proctor 36071* (BM, MO). GUATEMALA. ALTA VERAPAZ: Finca Mercedes, Teleman, Panzós, faldas da la Sierra de las Minas, quebrada Mercedes, 100 m, *Martínez S. et al. 22711* (MO); along Río Icvolaty, N and NW of Finca Cubilquitz to Quebrada Diablo, 300–350 m, *Steyermark 44752* (F); 1 mi. SW of Sibicte, vic. of Iaguana Sapala (Chajvovuch), 280 m, *Steyermark 44894* (F, UC). ESCUINTLA: SE of Escuintla, along or near Río Michatoya, 250–300 m, *Standley 89091* (F); between Panzós and Senahú, vic. of Cacão, 275 m, *Barber 6* (NY); Nazatenango, orillas del Río Grande, *Bernoulli 347* (B); Cubilquitz, *von Türckheim 8048* (B, NY, S). HUEHUETENANGO: Sierra de los Cuchumatanes, between Ixcan and Finca San Rafael, 200–800 m, *Steyermark 49389* (F). PETEN: W of Chinajá, along Río San Román, 50 m, *Steyermark 45507* (NY); along Río San Román, 50 m, *Steyermark 54407* (F); Sacatepequez, below Barranco Hondo, 1,100 m, *Standley 88974* (F). HONDURAS. ATLANTIDA: near Tela, Lancetilla Valley, 20–600 m, *Standley 52815* (F), *53554* (F); Mts. back of Puerto Sierra, *Wilson 161* (NY), *Wilson 577* (NY). NICARAGUA. CHINANDEGA: vic. of Chichigalpa, 90 m, *Standley 11234* (UC). CHONTALES: Castillo, Mar. 1893, *Shimek s.n.* (F, MO). MASAYA: Sierra de Managua, región de Las Nubes, *Standley 8744* (F). RIVAS: Isla de Ometepe, NW slope of Volcán Maderas, 800–1,000 m, 11°27′N, 85°31′W, *Stevens et al. 6582* (MO). ZELAYA: Cerro Baká, 6.5 km E of Río Coperna, 200–320 m, 13°40′N, 84°30′W, *Pipoly 4861* (MO). COSTA RICA. ALAJUELA: San Pedro de San Ramón, cerca del Río Barranca, *Brenes 21520* (CR). CARTAGO: Orosi, *Losch 770* (M); Finca Navarro, 1,350 m, *Maxon 623* (NY), *Maxon 641* (NY); 4 mi. SE of Turrialba, Las Animas RR station, 500 m, *Chrysler 5134* (MO, UC); near Río Naranjo, 2 km W of Orosi, 1,400 m, 9°48′N, 83°52′W, *Lent 4061* (AAU, CR, F, MO); Tapantí, ca. 15 km S of Paraíso, 1,150 m, *Mickel 1862* (NY), *2317* (NY); Carpintera, *Polakowsky 151* (B); Turrialba, slope of the Río Reventazón, behind the Instituto Interamericano de Ciencias Agrícolas, 600 m, *Mickel 2061* (NY), *3359* (NY). GUANACASTE: along Río Las Flores, between Quebrada Desprendimiento and Q. Sanguijuela, Hacienda Montezuma, 450 m, 10°40′N, 85°04′5″W, *Grayum et al. 4906* (MO). LIMON: near Río Sixaola ½ mi. SW of Bambú, ca. 3 mi. NE of Bratsi, 15 m, *Croat 43251* (MO, UC); lago sin nombre al pie de Fila Lleskila–Talamanca, 1,160 m, *Gómez et al. 23094* (AAU, BM,

MO, UC); base of hills on coastal side, between Punta Cocles and Punta Uva (E of Puerto Viejo de Talamanca), 20–60 m, 9°38′N, 82°43′W, *Grayum et al. 4419* (BM, MO, UC); Cordillera de Talamanca, ridge between Río Dantas (opposite mouth of Caño Seco) and Río Barbilla, 250–419 m, 10°00′5″N, 83°26′W, *Grayum et al. 8943* (MO); ca. 400 m upstream from where Bri Bri-Hone Ck. road crosses Río Sandbox, 70 m, *Moran 3092* (CR, F, MO); ca. 3 km SW of Suretka, RECOPE test drill site, 70 m, *Moran 3121* (MO); Chase, Talamanca, 300 m, *Ocampo S. 1637* (CR). SAN JOSE: ca. 7.5–8.5 km by road W of Ciudad Colón, ridge between Río Virilla and Quebrada Micos, along road between Finca Micos and Llano Limón, 550–650 m, 9°56′N, 84°18′W, *A. R. Smith et al. 1620* (MO, UC); 5 mi. S of Sta. María, 2,000 m, *Stork 1764* (MICH). PANAMA. CANAL AREA: near Frijoles, *Cornman 698* (UC); Barro Colorado Island, Shannon Trail, in creek no. 3, *Croat 8475* (F, NY); Frijoles, 30 m, *Killip 2810* (B, S), *2829* (S); along Río Indio de Gatún, 0–10 m, *Maxon 4868* (BM, S); Pipeline road, 8 km from main gate, *Mori & Kallunki 2826* (AAU, NY); 8 km NW of Gamboa, along Río Mendoza and small tributary, 0.5–1 km upstream from Pipeline Road bridge, 100 m, *Nee 7722* (U); 2–3.5 km N of Gamboa, along Quebrada San Antonio, 30–200 m, *Nee 9456* (AAU, U); Pearson Trail, *Shattuck 283* (F). CHIRIQUI: vic. of El Boquete, 1,000–1,300 m, *Maxon 5055* (BM, NY, S). COCLE: El Valle de Antón, 1,000 m, *Alston 8707* (BM). COLON: N of Diamante, ridge NW of abandoned mine on Quebrada de la Mina, 600–700 m, 9°24′N, 79°35′W, *Churchill & de Nevers 4242* (MO); near Porto Bello, 5–200 m, *Maxon 5733* (NY). DARIEN: Parque Nacional del Darién, ridge between Río Topalisa y Río Pucuro, ca. 17 km E of Pucuro, La Laguna area, 750–850 m, 8°3′5″N, 77°17′W, *Cuadros V. et al. 3895* (UC); near Cerro Pirre base camp, on Río Parasenico, 200–500 m, *Gentry & Clewell 7064* (MO); on Río Parasenico, 200–500 m, *Gentry & Clewell 7069* (MO); RENARE hut in Darién Natl. Park, 20 m, *McDonagh et al. 446* (BM); bank above Río Paca, *Stern et al. 705* (BM, NY, UC). PANAMA: at Río Tito, Península de Panamá, 275 m, *Ekman 15271* (BM, NY, S); Cordillera Central, Los Haitises, La Llanada, *Ekman 15485* (F, G, NY, S); Sta. Bárbara de Panamá, Península de Panamá, *Ekman 15836* (K, S); Tapia River, vic. of Juan Díaz, *Killip 2710* (S). CUBA. LAS VILLAS: Trinidad Mts., Santa Clara, El Porvenir, 650–750 m, *Britton & Wilson 5300* (NY); San Blas, La Sierra, Prov. Sta. Clara, 200–300 m, *Jack 7093* (MO, NY). ORIENTE: Loma del Gato, *Clement 757* (K, MICH, S, U, UC); Prov. directly S of Jaguey, Yateras, 420–510 m, *Maxon 4158* (NY, S), *Otto 176* (K); El Yunque, Mt. Baracoa, *Underwood & Earle 615* (NY); Baracoa, El Yunque Mt., *Underwood & Earle 989* (NY); prope villam Monte Verde, *Wright 1026* (G, K, L, MO, NY, S, UC), *Wright 1027* (G, K, L, UC); in 1859, 1860, *Wright 1086* (BM, G, K). JAMAICA. PROV. UNKNOWN: Wingfield ravine, 100–300 m, *Proctor 19252* (BM, MICH, U); in 1895, *Gilbert 54* (NY); Dollwood, *Harris 7374* (K); 1,200 m, *Harris 7374* (BM, NY), *Jenman 24* (K); Hartford and adjoining properties, near Priestman's River, near Cudjoe's Hole, *Maxon 2545* (NY). ST. THOMAS: 500–700 m, *Maxon 9057* (NY); John Crow Mts., E of Seamen's Valley, Portland Parish, 200–425 m, *Maxon & Killip 244* (BM, F, NY). PORTLAND PARISH: valley of Trafalgar River, near Jumbe Spring, 800 m, *Maxon & Killip 772* (BM, F, NY); Chepston Ridge, above Mt. Hermon, 6 mi. inland from Hoper Bay, *Moore 7* (NY); Chepstow Ridge, St. Georges, *Moore s.n.* (NY); Moy Hall, *Orcutt 6835* (UC). TRELAWNY PARISH: 5 mi. N of Quick Step, above Aberdeen P.O., Cockpit country, *Proctor 4069* (MO); 1.5–2 mi. SW of Ecclesdown, E slope of the John Crow Mts., 500–600 m, *Proctor 22690* (BM, MICH, U); Doll Wood, near Silver Hill Gap, 1,000 m, *Underwood 2304* (NY); Mansfield, near Bath, *Underwood 2802* (NY). DOMINICAN REPUBLIC. Liali, 100–500 m, *Abbott 2627* (GH); ravine 0.2 mi. SE of S Chiltern Estate, 300 m, *Lellinger 517* (MICH, MO, UC); Santo Domingo, prope Barahona, 350 m, *von Türckheim 2824* (BM, G, K, L, M, NY); Cordillera Central, La Cumbre, 300 m, *Ekman 14338* (S). HAITI. Massíf du Nord, Morne Cheneau, near Poitean, 400 m, *Ekman 4430* (S); Massíf des Cahos, Hinche, Morne Vaillecite, 600 m, *Ekman 6106* (S); Massíf de la Tloffe, eastern group, Mt. Calumelle, 1,200 m, *Ekman 7332* (S); vic. of St. Louis du Nord, *Leonard & Leonard 14363* (NY); Port Margot to Correil, 400–500 m, *Nash 199* (NY). PUERTO RICO. Luquillo Mts., *Wilson 280* (F, NY). MONTSERRAT. In Oct. 1879, *Holme s.n.* (K). ST. KITTS. 1889, *Berkeley s.n.* (NY). GUADELOUPE. In 1868, *Husnot 338* (K), *L'Herminier 18* (K); bois du Maine Gommer, bod du Galion, 400–600 m, *Duss 4199* (NY). DOMINICA. *Imray 120* (K); Rosalie, *Lloyd 699* (NY); Trafalgar Falls, *Whitefoord 6164* (BM). MARTINIQUE. Hautenis boisies de la Riviere, 400–500 m, *Duss 1635* (NY). ST. LUCIA. Upper Roseau River, 300 m, 18 Feb. 1936, *Box 464* (BM); Nov. 1883, *Murray 26* (K). GRENADA. ST. MARK PARISH: NW slope of Mt. St. Catherine, 500–600 m, *Proctor 17250* (U); near trail to Concord Falls, 360 m, *Seifert 42* (Z); no locality, *Sherring 87* (K, NY). ST. VINCENT. ST. ANDREW PARISH: Lowrt, 400 m, *Cooley 8393* (S). PROV. UNKNOWN. *Jenman s.n.* (NY); *H. H. Smith 1362* (BM); in 1890, *Smith 358* (G); 1890, *H. H. Smith & G. W. Smith 1121* (K, NY); forest above S end of the island, 300 m, *H. H. Smith & G. W. Smith 961* (K). TOBAGO. Campbelton woods, Charlotteville, *Broadway 3026* (B, BM, F, G, MO, NY, S, Z); Castara woods, *Broadway 4212* (BM, G, K), *7180* (BM, F, K, MO, S, Z); in 1889, *Hart 4166* (K); near Parrot Hall, ca. 2 mi. SW of Parlatuvier, 50 m, *Jermy 11370* (BM); Blue Basin, *Johnston 161* (BM); forest reserve of Main Ridge, 300 m, *Sandwith 1833* (BM, NY). TRINIDAD. North Post to Maqueripe, *Britton et al. 909* (F); Maracas, in the ground near waterfall, *Broadway s.n.* (K); Camaron Waterfall, *Cruger 44* (B); Leotode Est. Oropouche, Cave Forest, on limestone hill, *Fay 665* (BM); no locality, *Hart 205* (S); Maracas Falls, *Johnston 74* (BM); Simla Research Station, ca. 4 mi. N of Arima, 250 m, *Mickel 9516* (NY); without locality, *Prestoe 714* (BM, MO). FRENCH GUIANA. ININI: Inini River, en aval de degrad Fourmi Camp de base vers les Monts de l'Inini, *Cremers et al. 8780* (B, BR, F, Z); Montagne de l'Inini, extremité NW, 550 m, 3°30′40″N, 53°36′W, *Cremers et al. 8900* (F, U, Z); Montagne de l'Inini, zone central, extremité NW, 350–400 m, 3°31′N, 53°35′W, *Cremers et al. 9314* (B, F, Z); Mont Galbao, Cirque central, Haute Crique Makouali, 350 m, 3°35′N, 53°18′W, *de Granville et al. 8947* (BM, F, NY, Z). VENEZUELA. ANZOATEGUI: NE of Bergantin, Quebrada Negra, tributary of Río Zumbador, 500 m, *Steyermark 61143* (F, MO). ARAGUA: prope Coloniam Tovar, *Fendler 136* (B, G, GH, MO, NY). BOLIVAR: limites con el Territorio Federal Delta Amacuro, 36 km al NW de El Palmar, 350 m, 8°25′N, 62°00′W, *Aymard C. 5274* (UC), *5297* (MO). DISTRITO FEDERAL: Caracas, Chacao, *Otto 609* (B, G, K). FALCON: Dtto. Silva, Hacienda Montesco-Silencio, ca. 10 km NW de Tucacas, Cerro

Sanare, 100 m, *Burandt 715* (UC); Dtto. Federación, Parque Nacional "Cuevas de la Quebrada El Toro," 500–600 m, *Quijada 103* (NY); Sierra de San Luis, arriba de la Chapa, 900 m, 24 Mar. 1979, *van der Werff 3403* (UC). MERIDA: Mérida, *Moritz 365* (B, BM). MIRANDA: Cerros del Bachiller, near E end, Quebrada Corozal, S of Santa Cruz, 20–65 m, 10°9′N, 65°48′W, *Steyermark & Davidse 116306* (MO, UC). PORTUGUESA: Dtto. Apure, en los rios Bocoy y Riecito, limite entre estados Lara y Portuguesa, 800–1,200 m, 9°37′N, 69°25′W, *Ortega & Aymard 1818* (UC); Dtto. Guanare, entre Chabasquen y Córdoba, 1,250 m, *Ortega & Stergios 1467* (UC); Dtto. Sucre, Los Paramitos, a 20 km por aire al SO de Biscucuy, 1,000–1,500 m, 9°20′N, 69°05′W, *Ortega et al. 1886* (MO, NY, UC). SUCRE: *Ortega et al. 1845* (MO); Dtto. Cagigal, near border with Dtto. Arismendi, 850 m, 10°39–40′N, 62°43′W, *Steyermark et al. 121514* (MO, NY, UC); in 1846, *Moritz 23* (G). ZULIA: Dtto. Mara, cuenca del Río Guasare, alrededores del Destacamento Guasare no. 1 (La Yolanda), 200–250 m, 10°52′N, 72°29′W, *Bunting et al. 12036* (UC); SW de Machiques, a lo largo de la Quebrada Perayra, afluente del Río Tokuku, SE de la Misión de Los Angeles de Tokuku, 450–475 m, *Steyermark 99872* (MO). COLOMBIA. ANTIOQUIA: near Guapá, 53 km S of Turbo, 60 m, *Haught 4627* (NY, S); Boquerón, *Kalbreyer 1916* (B); Titiribí, *Kalbreyer 1499* (B); Urrao, Vereda Calles, Parque Nacional de Las Orquídeas, cabana del INDERENA en Río Calles, quebrada La Agudelo, 1,450 m, *Callejas et al. 2841* (NY); Tocarema, 2,200 m, *Lindig 236* (BM). CHOCO: carretera San José del Palmar-Novita, entre La Italia (pueblo nuevo) y Curundo, 430–450 m, *Forero & Jaramillo 2134* (MO); near Caserío La Teresita, 0.5–2.5 km N of the INDERENA Camp on the Río Truando, 50–100 m, *Lellinger & de la Sota 550* (COL); Atrato, *Schott 51* (F, MO), *755* (MO); Parque Nacional Natural Los Katíos, sector Tilupo camino del Salto, *Zuluaga R. 332* (COL). MAGDALENA: Santa Marta, Finca El Recuerdo, Boca Toma Forest, 800 m, *Bennett 20* (F); Finca Los Arroyitos in quebrada N of house, 1,800–1,900 m, 10°56′N, 73°58′W, *Kirkbride 2368* (COL); 1,000 m, *H. H. Smith 2450* (BM, F, MICH), *958* (BM, MICH, S). CUNDINAMARCA: Pueblo Nuevo, quebrada "La Guayacana," 900–950 m, *Murillo 363* (COL). NORTE DE SANTANDER: Ocaña, 2,000 m, *Kalbreyer 317* (B, K); 1846–1852, *Schlim 397* (B, BM, G). SANTANDER: Espíritu Santo, 1,800 m, *Kalbreyer 317* (B). TOLIMA: Cajamarca, between Ibague and Cajamarca, 2,000 m, *Alston 7716* (MO). VALLE: La Margarita, Río Digua Valley, 760 m, *Killip 34888* (COL). ECUADOR. ESMERALDAS: near San Mateo, road to Esmeraldas airport, gravel road 8.6 km beyond bridge, over Río Esmeraldas, 80 m, 0°52′N, 79°33′W, *Croat 55623* (F, MO). LOS RIOS: Río Palenque Biological Station, km 56 Quevedo–Sto. Domingo, 150–220 m, *Evoy 61* (NY), *Lojtnant 15757* (AAU). MANABI: El Recreo, *Eggers 15118* (BM, F, L, M), *15175* (F). MORONA-SANTIAGO: cerca la Parroquia de Bomboiza, en la carretera Gualaquiza–Zamora, alrededores del puente sobre el Río Bombioza, 800 m, *Baker & Zaruma 6476* (MO, NY). NAPO: Parque Nacional Yasuní, Anangu, 260–350 m, 76°23′W, 0°31–32′S, *Øllgaard et al. 39205* (AAU, NY). PICHINCHA: Loc. 170–175, Sto. Domingo–Quinindé, 300 m, *Acosta S. 13783* (F). PERU. AMAZONAS: Bagua, 12 km E of La Peca, 1,700 m, *Barbour 2500* (F). HUANUCO: Leoncio Prado. La Cueva de las Pavas, 5 km S de Tingo María, Dtto. Rupa Rupa, 672 m, *Schunke V. 3261* (F); Tingo María, on steep rocky slope above Río Huallaga, *Croat 21082* (MO); hills above river on steep limestone forested slope, 650 m, *Moran 3683* (MO), 700 m, *Tryon & Tryon 5228* (BM, F). JUNIN: Cochero, 1,780 m, *Pavón 186* (G); Chanchamayo, 1,500 m, *Schunke 20* (S), *4909* (BM); area of Pichita Caluga, *Walden 84* (BM). PASCO: Oxapampa, 50 km from Oxapampa, Río El Tunqui, 1,620 m, 75°30′W, 10°15′S, *Smith et al. 1710* (MO). SAN MARTIN: Juan Jui, Alto Río Huallaga, 400–800 m, *Klug 4253* (BM, F, MO, NY, S). BOLIVIA. LA PAZ: Prov. Iturralde, Tumupasa, 500 m, *Williams 1076* (NY, UC); 600 m, *Williams 1076a* (NY). COCHABAMBA: Prov. Chapare, vic. of Villa Tunari, along Río Espírito Santo, on trail to Baja Copacabana, 16°57′S, 65°25′W, *Croat 51271* (MO). LA PAZ: Prov. Nor Yungas, Polo-Polo bei Coroico, 1,100 m, *Buchtien 3334* (S). BRAZIL. STATE UNKNOWN: no locality given, *Mendonca 1208* (B). PARA: Macau airstrip, 1.5 hours upstream from Lageira airstrip, on Rio Maicuru, 0°55′S, 54°26′W, *Strudwick et al. 3574* (NY). RIO GRANDE DO SUL: Sta. Cruz, *Jürgens 27* (MICH). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 5318* (B). SÃO PAULO: São Paulo, *Mosen 3736* (S). ARGENTINA. SALTA: Parque Nacional El Rey, *Brown 1338* (MO).

Asplenium laetum grows terrestrially in deeply shaded forests or on boulders along streams. It is the most common and widely distributed species of section *Hymenasplenium* in the New World (Map 4), ranging from Mexico to northern Argentina, but absent from most of Amazonia. The species has sometimes been reported from Africa and Madagascar, but these reports are based on specimens of *A. inaequilaterale* Willd., a species that does not belong to section *Hymenasplenium*.

The species is characterized by dark petioles and rachises, short-creeping rhizomes, and attenuate lamina apices (Fig. 8A). In other characters it is extremely variable. Some single-character variation is correlated with geography. For example, plants from the Canal Area in Panama usually have obtuse or retuse pinnae with nearly entire or shallowly serrate margins (e.g., *Croat 7008*, *Kennedy 2673*, *Béliz 150*). Plants from Bolivia and Peru have attenuate pinna apices with sharply and obliquely serrate margins (e.g., *Croat 51271*, *Klug 4253*, *Schunke V. 3261*). We have not, however, subdivided the species because no other characteristics correlate with this variation, nor are there any suites of quantitative characteristics that correlate with geography (Fig. 9). Future studies, especially of isozymes and chromosomes, may show that *A. laetum* as circumscribed here actually consists of several species.

Occasional specimens will key to *A. laetum* that are actually intermediate between *A. delitescens* and *A. laetum* (Fig. 6B). Such intermediate specimens are treated in the hybrid section of this monograph.

Several species of *Asplenium* that do not belong

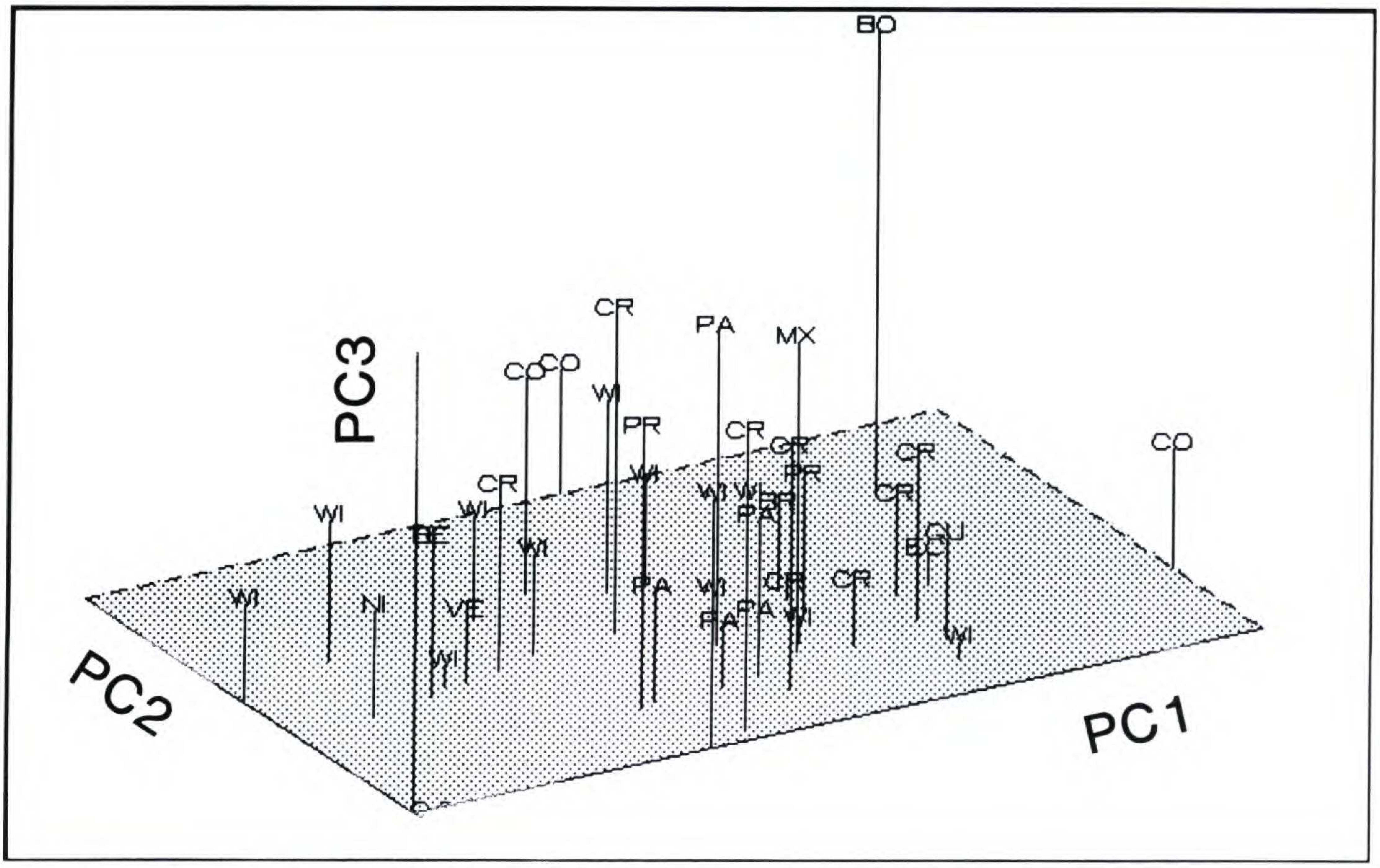


FIGURE 9. Principal Components Analysis of 30 characters of *Asplenium laetum*. BE, Belize. BR, Brazil. BO, Bolivia. CO, Colombia. CR, Costa Rica. EC, Ecuador. GU, Guatemala. NI, Nicaragua. PA, Panama. PR, Peru. VE, Venezuela. WI, West Indies.

to section *Hymenasplenium* are frequently misidentified as *A. laetum* because of their similarity in leaf cutting and outline (i.e., *A. argentinum* Hieron., *A. hostmannii* Hieron., and *A. otites* Link). These species can be distinguished from *A. laetum* by their erect rhizomes and greenish petioles. Besides these characteristics, they also differ from *A. laetum* in the form of the rachis and costa junctures. *Asplenium laetum* has the form typical of section *Hymenasplenium*: the costa is slightly sunken and bordered by a flange of green tissue that is decurrent on the adaxial surface of the rachis, and the decurrent margin of the pinna is not thickened (Fig. 16D). In contrast, the other *Asplenium* species mentioned above have prominulous costae not bordered by a flap of green tissue, and the decurrent margins of the pinnae are thickened and often a lighter color than the rest of the laminar tissue (Fig. 16C).

4. Asplenium obtusifolium L., Sp. Pl. 1080. 1753. *Asplenium riparium* Liebm. var. *obtusifolium* (Klotzsch & Karsten) Hook., Sp. Fil. 3: 119. 1860. TYPE: Petiver, Pter. Amer. 117, t. 2, fig. 14 (erroneously cited by Linnaeus as f. 4). [= Plumier, Traité Foug. Amér. t. 67. 1705.] Based on a plant from Morne de la Calebasse, Martinique. Figure 10; Map 5.

Asplenium aquaticum Klotzsch & Karsten, Linnaea 20: 354. 1847. *Asplenium obtusifolium* var. *aquaticum* (Klotzsch & Karsten) Giesenhagen, Flora 76: 172, fig. 1. 1892. TYPE: Colombia. "In locis paludosis," *Karsten s.n.* (holotype, B; photo, GH ex B).

Plants epilithic; roots 0.6–1 mm wide; rhizome 2.5–4.5 mm wide, nearly naked, the projecting apex sparsely scaly; scales 0.9–1.3 × 0.15–0.4 mm, brown, deltate-acuminate; petiole base 1.5–3.5 mm wide, swollen, 1.5–5 mm distant from each other on the same row; petiole 4–10.5 × 0.1–0.25 cm, ⅓–½ the leaf length, terete, greenish, fleshy and dull, glabrous; lamina 8–20 cm long, dark green, translucent, 1–2-pinnate (lowest pair of pinnae usually lobed or divided basally), deltate to oblong with subconform apex; rachis like petiole, narrowly marginate adaxially; lateral pinnae 2.5–4.5 × 0.8–1.5 cm in the middle of the leaf, 3–10 pairs, slightly to strongly ascending, obliquely oblong to oblong-lanceolate, often laciniate basally into 1–3 segments, simply toothed, the teeth 0.5–1.5 mm long, the basiscopic margin excavate ca. ½ the pinna length, the apex usually obtuse, rarely acute, auricle 1–2.5 mm long; veins 1-forked at middle part of pinnae; sori 4.5–9 mm long; spores papillate, 27–33 μm long for race with 64 spores per sporangium, 42–47 μm long for race with 32 spores per sporangium.

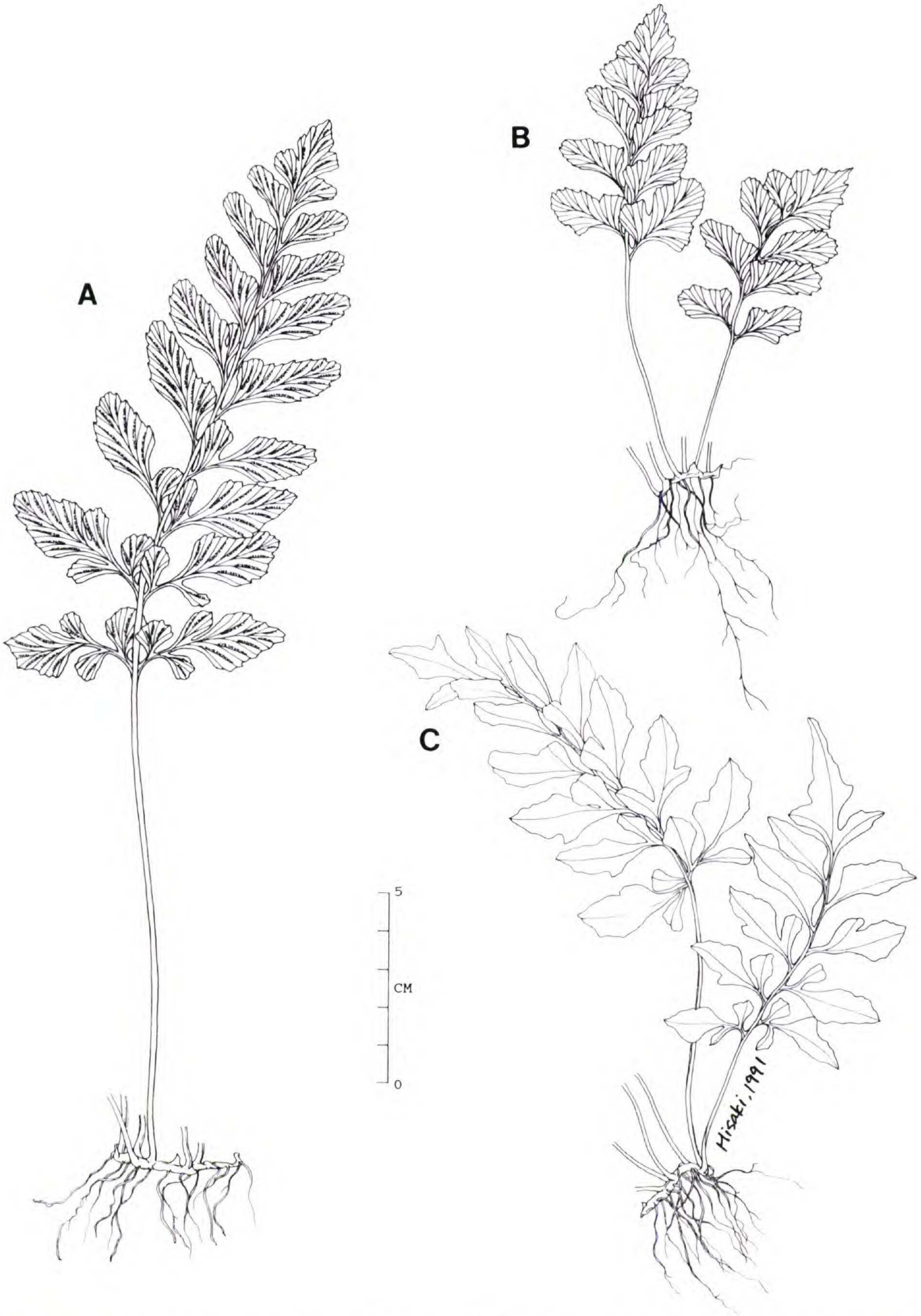
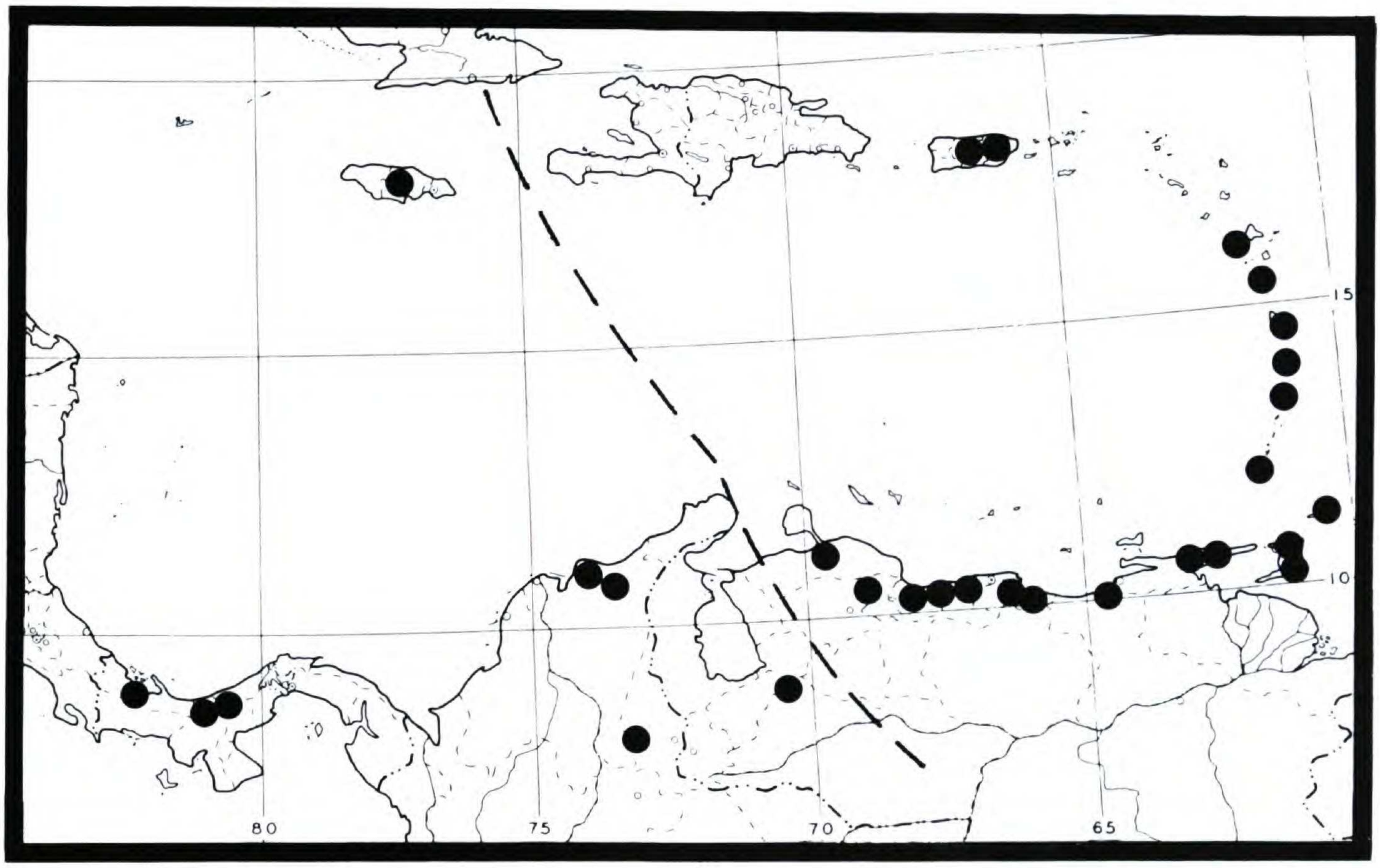


FIGURE 10. *Asplenium obtusifolium.*—A. Colombia, *H. H. Smith 1126* (NY).—B. Venezuela, *van der Werff 702* (MO).—C. Grenada, *Sherring 131* (K).

Additional specimens examined. PANAMA. BOCAS DEL TORO: 6.3 mi. N of bridge over Fortuna Lake, between Fortuna and Chiriquí Grande, 2.2 mi. N of Continental Divide, 820 m, 8°45′N, 82°16′W, *Croat & Grayum 60385* (AAU, MO, UC); Fortuna Dam region, along road to Chiriquí Grande, 950–1,000 m, 8°48′N, 82°10′W, *McPherson 8666* (MO). COCLE: El Copé, forest on Continental Divide above town, 700–900 m, 8°38′N, 80°38′W, *Hammel 13645* (MO, UC). VERAGUAS: vic. of Escuela Agrícola, Santa Fé, near trail to top of Cerro Tute, along stream, 800 m, *Antonio 3530* (MO); 11–13 km beyond Agricultural School at Santa Fé, valley of the Río Dos Bocas, 350–500 m, *Croat 25732* (MO); 6.5 km from Santa Fé, base of Cerro Tute, *Folsom 3062* (MO);



MAP 5. The distribution of *Asplenium obtusifolium*. The 32-spored race occurs west of the dashed line; the 64-spored race occurs east of the dashed line.

NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3964* (MO). PUERTO RICO. Toro Negro, 1936, *Quick s.n.* (MICH); prope Utuado, *Sintenis 6271* (B, BM, G, S), *6443* (B, BM, G, K, L, NY), *6533* (B, BM, G, GH, K, L, S); Toro Negro, 50 km WSW of San Juan, *Tryon 7399* (BM, GH, MO, NY). GUADELOUPE. No locality, *L'Herminier s.n.* (B, BM, GH, L, MO, NY); in 1862, *L'Herminier 79* (B, BR, G, K), *169* (L). DOMINICA. Rosalie, 1903, *Lloyd 698* (NY); Mt. Diablotin, *Lloyd 871* (NY); path from Fresh Water Lake to Boeri Lake, 800 m, *Shillingford & Adams 98* (MO); Sylvania Estate, gorge between the estate house and orange plantation, 488 m, *Hodge 1092* (GH); NE slopes of Morne Diablotin, 800 m, *Hodge & Hodge 2793* (GH), *Imray 13* (K); St. David Parish, along Boeri Lake Trail near Fresh Water Lake road, 1,200 m, *Lellinger 571* (GH); near Boeri Lake, *Whitefoord 4174* (BM); NW slopes of Morne Diablotin, *Whitefoord 4549* (BM); slopes of Micotrin, along path NW of Fresh Water Lake toward Boeri Lake, 900 m, *Wilbur et al. 7473* (F); St. Domingo, Morne Gonivo, 900 m, *Eggers 608* (B, BR, G, L, MICH, S, UC); no locality, in 1843, *Bory s.n.* (L). MARTINIQUE. Jan. 1868, *Hahn 68* (B, BM, G, GH, K, S); Calebaye, *Belanger 801* (B, G); no locality, *Duss 1636b* (F, G, GH, MO); bois des Barris-Taunes, 450–800 m, *Duss 4205* (NY); no locality, *Husnot 334* (B, BM, BR, F, G), *Pitard s.n.* (G). ST. LUCIA. Savanne Edmund District, SE of Piton Troumassée, 600–650 m, *Proctor 17703* (U); Morne Calebasse, N of Morne Rouge, 650–760 m, *Proctor 21691* (GH, U); no locality, *Sieber 363* (BM, M); in 1833, *Sieber s.n.* (BR, G); source of Canaries River, 800 m, *Box 456* (BM); Upper Roseau River, 300 m, *Box 473* (BM); St. Georges, Annandale, *Broadway s.n.* (BR, F, K, NY). ST. VINCENT. Majorca estate, 400 m, *Harrison SVT174F* (BM); Lisdara, *Hodge 2410* (GH, NY); upper valley of Richmond River, 330–540 m, *Morton 6170* (GH); without locality, *Smith & Smith 710* (BM). GRENADA. *Sherring 131* (K, NY); NW slope of Mt. St. Catherine, 500–700 m, *Proctor 17254* (GH). TOBAGO. Vil-el-Karst, main ridge, *Broadway s.n.* (BR, G, GH, MO, S); Roxborough–Parlatuvier road, near 5th milepost, 300 m, *Sandwith 1790* (BM). TRINIDAD. Maracas waterfall, *Britton et al. 1656* (GH, NY); Maracas, *Broadway 5353* (BM, BR, F, MO, UC); Maracas Falls, 200 m, *Fay 673* (K); in 1877–1880, *Fendler 139* (B, BM, G, GH, K, MO, NY, S, UC), *Hart 241* (S), *Holdridge 50* (K), *Hombersley 68* (BM); Las Cuevas, *Hombersley 390* (BM); 7 mi. N of Arima, Asa Wright Nature Centre, 400 m, *Mickel 9446* (NY). VENEZUELA. ANZOATEGUI: NE of Bergantín, Quebrada Negra, tributary of Río Zumbador, 500 m, *Steyermark 61148* (F, G, MICH, MO, NY, S); Cerro Los Pajaritos, between Cerro San José and Cerro Peonía, along headwaters of Quebrada La Tigra, 1,500–1,600 m, *Steyermark 61569* (G). ARAGUA: Henri Pittier National Park, road between Maracay and Ocumare de la Costa, 3 km N of summit, 970 m, 10°20′N, 67°34′W, *Croat 60574* (MO); prope Coloniam Tovar, *Fendler 131* (BR, G, GH, K, MO, NY); Colonia Tovar, *Moritz 384* (B, BM, BR, P, photo GH, MICH ex P); Rancho Grande, 1,000 m, *Pannier 132* (M). BARINAS: Dtto. Bolívar, entre Sto. Domingo y Altamira, en el sitio denominado Quebradón, 1,300–1,500 m, *Ortega & van der Werff 2358* (NY, UC), *Ortega & van der Werff 2348* (M). CARABOBO: arriba de Los Tanques y La Toma, entre Quebrada no. 2 y Quebrada de los Verros, en las laderas arriba de las cabeceras del Río San Gián, 750–900 m, *Steyermark & Steyermark 95249* (NY). DISTRITO FEDERAL: Depto. Libertador, entre La Peñita y Chichiriviche, a lo largo del Río Chichiriviche, 450 m, 10°31′N, 67°14′30″W, *Steyermark & Espinoza 112683* (MO, NY). FALCON: Sierra

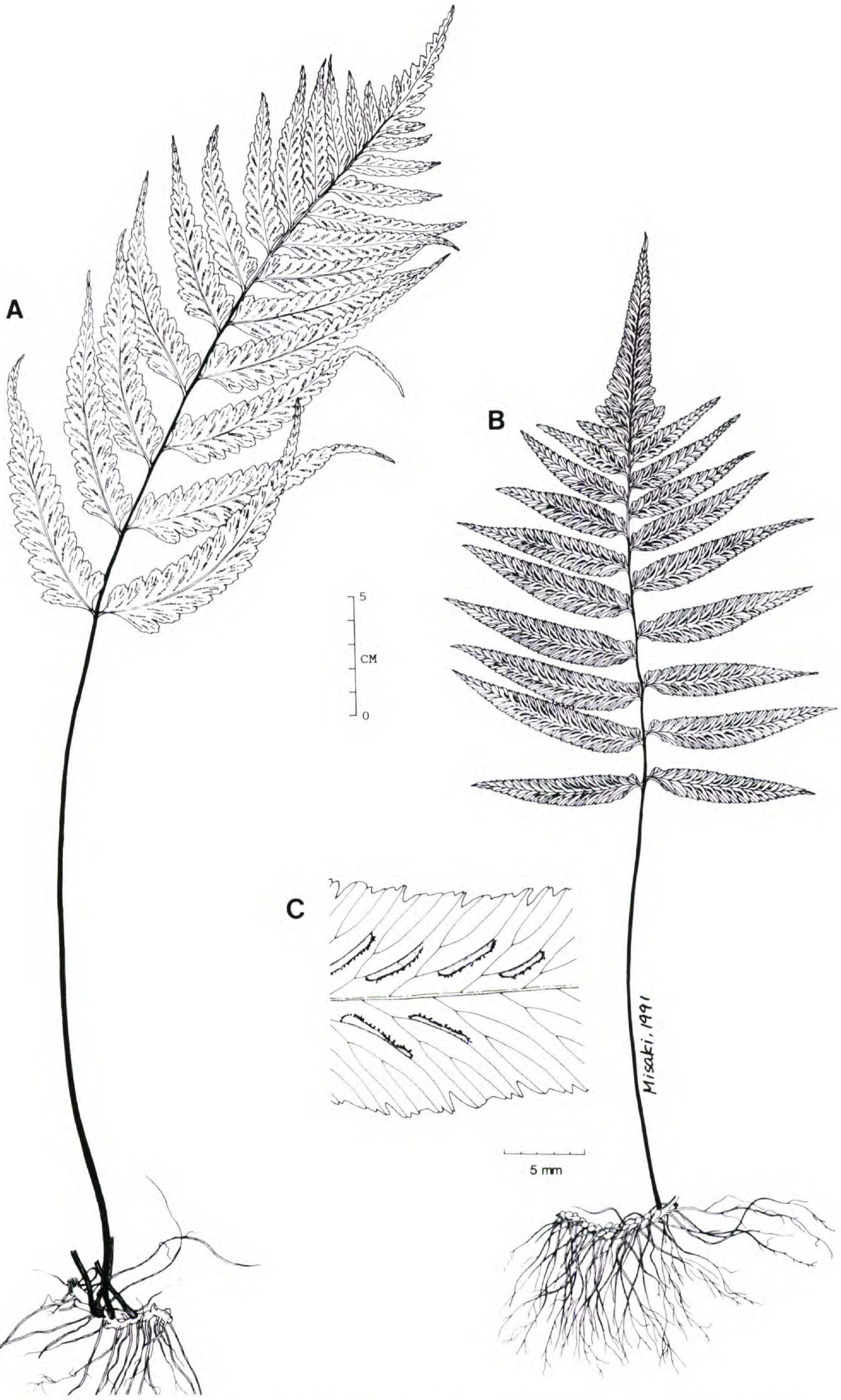


FIGURE 11.—A. *Asplenium purpurascens*, Ecuador, *Holm-Nielsen et al. 2720* (AAU).—B, C. *A. ortegae*, Venezuela, *van der Werff & González 4599* (MO).

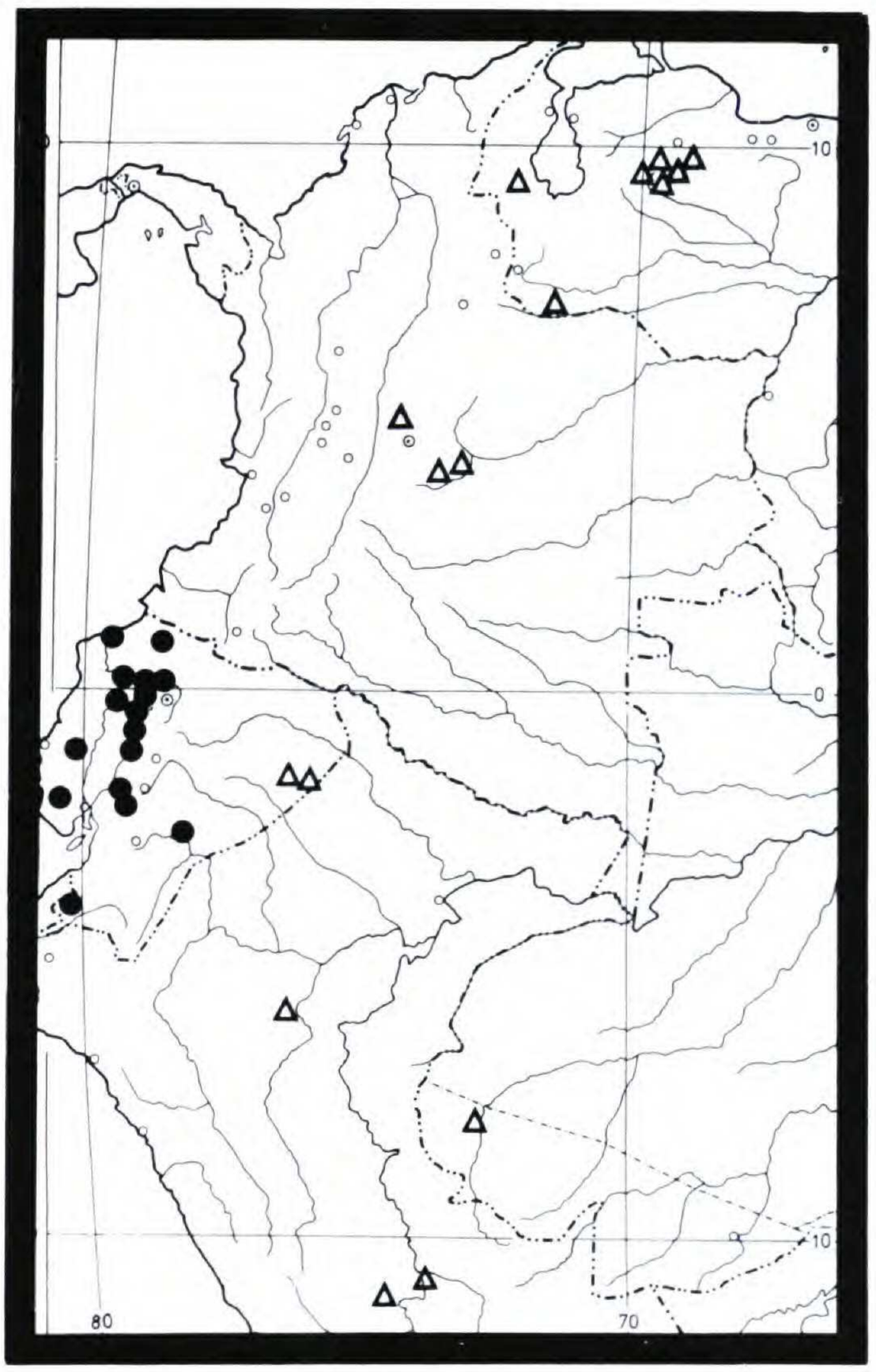
de San Luis, arriba de La Chapa, 1,200 m, *van der Werff & TR 702* (UC). LARA: area limítrofe entre Lara y Yaracuy, Dttos. Urdaneta y Bolívar respectivamente, en la Fila Azul y Hda. El Jaguar, 700–900 m, *Ortega & R. F. Smith 2440* (UC). MIRANDA: Dtto. Paéz, Fila La Tigra, Hda. San Juan, 18 km SW de Cúpira, 650 m, 10°04–05′N, 64°45′W, *Ortega & González 365* (MO, NY, UC); Cerros del Bachiller, above Quebrada Corozal, S of Sta. Cruz, 10 km W of Cúpira, 600 m, 10°9′N, 65°48′W, *Steyermark & Davidse 116896* (MO, UC). SUCRE: Península de París, Cerro de Humo, ca. 14 km N del pueblo de Río Grande Arriba, arriba de Boca de Cumaná y Punto Siparo, NE de Irapa, 1,060 m, *Steyermark 94822* (NY); Península de Paria, Cerro de Río Arriba, W de Cerro de Humo, a lo largo de Río Santa Isabel, arriba de Santa Isabel, 600–700 m, *Steyermark & Rabe 96232* (NY); Dtto. Cagigal, Península de Paria, near border with Dtto. Arismendi, low trail between El Paujil and El Brasil, 850–890 m, 10°39–40′N, 62°43′W, *Steyermark et al. 121451* (MO, NY, UC); Dtto. Arismendi, Península de Paria, between Tacarigua and Río Tacarigua, E of Cerro de Humo, 560 m, 10°41–42′N, 62°36–37′W, *Steyermark et al. 121590* (MO, UC). COLOMBIA. PROV. UNKNOWN: *Karsten s.n.* (B). MAGDELENA: Sierra Nevada de Santa Marta, Alto Río Buritaca, Alto de Mira, 900–1,100 m, *Madriñán & Barbosa 258* (GH, MO); Sierra Nevada de Santa Marta, edge of Quebrada La Sirena, 1,100 m, 10°59′N, 73°59′W, *Kirkbride 2188* (COL, NY, UC); Santa Marta, above Onaca, 1,100 m, *H. H. Smith 1126* (B, BM, BR, COL, G, GH, L, MICH, MO, NY, S, UC). NORTE DE SANTANDER: Ocaña, 1,600 m, *Schlim 653* (B, BR, G, K, L). SANTANDER: Tequendame, 1,200 m, *Kalbreyer 951b* (B).

Asplenium obtusifolium has a circum-Caribbean distribution (Map 5). It grows in the spray of, or underneath, waterfalls and on wet rocks along shaded streams. Its elevational range is 200 to 1,200 m.

This species is characterized by greenish petioles, fleshy leaves, small (8–20-cm-long) laminae, and few (3–10) pinna pairs. The pinnae are usually obtuse and the basal pairs lobed or divided basally (Fig. 10).

Asplenium obtusifolium is remarkable by having two races: one with 32 spores per sporangium, the other with 64 spores. The sporophytes of the two races appear indistinguishable and could not be distinguished by a Principal Component Analysis of 20 quantitative morphological characters (Fig. 5). The two spore races differ geographically, with the 32-spored race occurring only in the western portion of the range and the 64-spored race occurring only in the eastern portion (Map 5).

The 32-spored race is presumably apogamous, but this idea needs to be investigated. In the Old World, *A. apogamum* Murakami & Hatanaka, *A. cheilosorum* Kunze, and *A. hondoense* Murakami & Hatanaka have been shown to have both a sexual race with 64 spores per sporangium and an apogamous race with 32 spores per sporangium (Mitui et al., 1989). Therefore, it seems likely that the 32-spored race of *A. obtusifolium* is apogamous.



MAP 6. The distribution of *Asplenium purpurascens* (solid dots) and *A. ortegae* (open triangles).

5. Asplenium ortegae Murakami & R. C. Moran, sp. nov. TYPE: Venezuela. Apure: Dtto. Paéz, along Río Arauca at Colombian border, *van der Werff & González 4599* (holotype, MO; isotype, NY). Figure 11B, C; Map 6.

Plantae terrestres. Rhizoma 3.5–5.2 mm latum, internodiis approximatis, squamis 0.5–1.9 mm longis, ca. 0.2 mm latis, lanceolatis, clathratis, brunneis vel nigriscentibus, 3–6-cellulas latis. Petioli 6–21 cm longi, atrobrunnei, nitidi, sparse squamulosi; laminae 11–25 cm longae, 9–18 cm latae, deltatae vel late oblongae, ad apicem abrupte angustatae, segmento terminali lobato, elongato; pinnae plerumque 4.5–9 cm longae, 1.1–1.7 cm latae (pinnae basales interdum profunde lobatae et usque ad 3 cm latae), 6–10-jugatae, breviter petiolatae vel sessiles, latere acroscopico basali truncato, rotundato vel (in Amazonia occidentali) cuneato, nunquam auriculato, latere basiscopico basali cuneato vel excavato, marginibus typice serratis vel serrate lobulatis, interdum in foliis maximis usque ad costas, apice longe attenuatis. Rhachis basaliter atrobrunnea vel nitida, distaliter viridula, infra sparse squamulosa vel glabrata. Venae (2–)3–4-furcatae. Sori 3–7 mm longi.

Plants terrestrial; roots 1.1–1.7 mm wide; rhizome 3.5–5.2 mm wide, nearly naked; scales 0.5–1.9 × 0.23–0.29 mm, black-brown, lanceolate; petiole base 2.2–5.5 mm wide, swollen, 0.5–1.1 mm distant from each other on the same row; petiole 6–21 × 0.09–0.15 cm, ⅓–½ the leaf length, atropurpureous, sparsely scaly at base; lamina 11–25 cm long, light green, herbaceous, 1-pinnate, deltate to oblong with acuminate apex, apex pinnatifid, abruptly reduced or evenly tapered; rachis green to dark reddish purple, grooved with green herbaceous wings perpendicular to the plane of the lamina; lateral pinnae 5–9 × 0.9–1.7 cm in the middle of the leaf, 6–10 pairs, lanceolate to linear-lanceolate, the margin slightly double-toothed, 0.5–1.3 mm deep, the basiscopic side excavate for 1/10–⅕ the length of the pinnae, stalked at lower pinnae, auricle absent; veins 3–4 times forked; sori 3–7 mm long; spores about 30 μm, 64 per sporangium, perispore cristate.

Paratypes. VENEZUELA. PORTUGUESA: Dtto. Ospino, Quebrada Honda, en el caserio La Cristobera, *Ortega et al. 3093* (BM); Dtto. Guanare, Mpio. Papelón, rivera izquierda del caño Iguez, *Pérez 1* (UC); Dtto. Guanare, terrenos del la UNELLEZ, una quebrada en la Mesa Alta, 9°4′N, 69°49′W, *Ortega 1912* (UC); Dtto. Araure, en los Ríos Bocoy y Riecito, límite entre los Estados Lara y Portuguesa, 800–1,200 m, 9°37′N, 69°25′W, *Ortega & Aymard 1817* (UC); entre Agua Blanca y Los Hijitos, 160 m, *Ortega & Aymard 2087* (NY); entre Agua Blanca y San Rafael, Quebrada Los Hijitos, 160 m, *Ortega & Aymard 2088* (UC); Dtto. Guanare, along road to San José de La Montaña, 500 m, 9°20′N, 69°43′W, *A. R. Smith et al. 1062* (UC); Boca de Monte, 23 km N del vado del Río Suruguapo, 38 km N por la autopista Guanare–Ospino, en sitio Las Marías, 400 m, 9°18′N, 69°43′W, *Steyermark et al. 127134* (MO, UC). ZULIA: Dtto. Perijá, 2 km W of the intersection of the Río Aricuaisá and the Maracaibo–La Fría Hwy. (Hwy. 6), 10 m, *Davidse et al. 18205* (MO, UC); Dtto. Colón, intersection of Río Catatumbo and La Fría–Maracaibo Hwy. (Hwy. 6), 30 m, 9°07′N, 72°37′W, *Davidse et al. 18826* (MO, UC); Dtto. Colón, intersection of Río Catatumbo and the La Fría–Maracaibo Hwy. (Hwy. 16), 30 m, *Davidse et al. 18826* (MO, UC); Boca de Monte, 23 km N del vado del Río Suruguapo, 38 km N por la autopista Guanare–Ospino, en el sitio Las Marías, 400 m, *Steyermark et al. 127131* (MO, UC). COLOMBIA. CUNDINAMARCA: Carretera Medina desviación a la izquierda, Río Humea, 500–550 m, *Murillo 2197* (MO). META: Río Guatiquia, *Lehmann 8830* (B); Puerto López, 240 m, *Little & Little 8427* (COL). ECUADOR. PASTAZA: Lorocachi, 2 km upriver on Río Curaray, opposite Military Camp, 200 m, 1°28′S, 75°58′W, *Brandbyge & Asanza C. 31225* (AAU); Ceilán, Pica from Ceilán to Río Cononaco, on the N side of Río Curaray, 200 m, 1°36′S, 75°40′W, *Brandbyge & Asanza C. 31649* (AAU, F, UC). PERU. JUNIN: Colonia Perene, 680 m, *Killip & Smith 24924* (F); Puerto Bermúdez, 375 m, *Killip & Smith 26633* (F). LORETO: Yurimaguas, lower Río Huallaga, 135 m, *Killip & Smith 29078* (NY). BRAZIL. ACRE: Cruzeiro do Sul, Rio Juruá and Rio Moa, between Mundurucus and Tatajuba, Rio Juruá, *Maas et al. P12902* (F).

Asplenium ortegae is named for Francisco Ortega, prominent Venezuelan pteridologist, who has given us much hospitality and assistance during fieldwork in Venezuela.

From Colombia to Bolivia, the species occurs on the eastern side of the Andes; in Venezuela, it occurs on both sides (Map 6). It grows on shaded forest floors in wet forests from 0 to 500(–800) m.

Asplenium ortegae is characterized by short-creeping rhizomes, atropurpureous petioles, truncately serrate-lobed pinna margins, and usually 3- or 4-forked veins (Fig. 11B, C). Rarely, the basal pinnae become pinnatifid, and the plants then resemble *A. purpurascens* (which also has atropurpureous petioles). The two species may be separated by the characteristics given in the key.

Despite the resemblance to *A. purpurascens*, evidence from chloroplast DNA supports a close relationship of *A. ortegae* with *A. delitescens* (this evidence will be presented in a future paper by the first author). Morphological characteristics also support this relationship. Both species have deltate laminae, relatively few (6–10) pinna pairs, and similarly shaped laminar apices. *Asplenium delitescens*, however, differs by having stramineous petioles, less serrate pinna margins, and twice-forked veins (Fig. 6A). It may eventually be shown that *A. ortegae* is of hybrid origin involving *A. delitescens* as one of its parents.

6. Asplenium purpurascens Mett. ex Kuhn, Linnaea 36: 102. 1869. TYPE: Ecuador. Chimborazo: "ad pedem montis Chimborazo," *Spruce 5697* (holotype, B not seen; fragment, B). Figure 11A; Map 6.

Asplenium melanopus Sodiro, Anal. Univ. Quito 9: 88. 1893 [= Crypt. Vasc. Quit. 189. 1897]. *Diplazium melanopus* (Sodiro) Hieron., Bot. Jahrb. Syst. 34: 456. 1904. SYNTYPES: Ecuador. Pichincha: "Crece en la región tropical, en los bosques de los Colorados," *Sodiro s.n.* (isosyntype, K); "en el valle de Pallatanga cerca de Puente de Chimbo," *Sodiro s.n.* (isosyntype, K).

Plants terrestrial; roots 1.5–2 mm wide; rhizome 4.2–6.5 mm wide, sparsely scaly; scales 1.6–2.3 × 0.35–0.55 mm, black to dark brown, lanceolate; petiole base 2–5 mm wide, swollen, 2–4 mm distant from each other on the same row; petiole 17–27 × 0.15–0.2 cm, about ½ the leaf length, dark reddish purple, scaly at base; lamina 20–30 cm long, dark green, firm-herbaceous, 1-pinnate, deltate, the apex attenuate, pinnatifid; rachis like the

petiole, grooved, with herbaceous green wings; lateral pinnae 6.5–12 × 1.3–2.5 cm in the middle of the leaf, 8–11 pairs, lanceolate to linear-lanceolate, long-acuminate, the basiscopic side excavate for ⅐–⅕ the length of the pinna, stalked at the lower pinnae, auricle absent, the margin lobed to pinnatifid, the tip of each lobe with rounded teeth, about 1 mm deep; veins 3–4 times forked; sori 4–8 mm long, often diplazioid; spores 27–33 μm, 64 per sporangium, perispore cristate.

Additional specimens examined. ECUADOR. CHIMBORAZO: vic. of Sacramento, on E side of Río Sacramento, 1,200–2,000 m, *Wiggins 11095* (NY, UC). COTOPAXI: Tenefuerste, Río Pilalo, km 52–53, Quevedo–Latacunga, 750–1,300 m, *Dodson & Gentry 12275* (MO, QCNE); 20 km NW of Corazón, Río Guapara, 250 m, *Sparre 17173* (S); in confiano Columbiae, *Buchwald 43* (UC); El Recreo, *Eggers 15214* (B, BM, L). ESMERALDAS: near San Mateo, road to Esmeraldas airport, gravel road 8.6 km beyond bridge over Río Esmeraldas, ca. 6.6 km beyond Univ. Luis Vargas Torres Est. Exp. Mutile, along Río Mutile, 80 m, 0°52′N, 79°33′W, *Croat 55622* (F, MO, UC). GUAYAS: near Bucay, western cordillera, junction of the provinces of Guayas, Canar, Chimborazo, and Bolívar, 300–400 m, *Camp 3785* (F, GH, NY); Loma Alta, Cerro de Vacas Muertas, Cordillera de Colonche, 250 m, *Valverde 510* (MO). LOJA: W of El Limo, Alamor–Cazaderos Road, 1,400 m, *Harling & Andersson 22310* (F). LOS RIOS: Río Palenque Biological Station, km 56 Rd. Quevedo–Sto. Domingo, 150–220 m, *Dodson & Gentry 10051* (MO, QCNE); ca. 40 km E of Babahoyo, surroundings of Montalvo, 100–200 m, 1°47′S, 79°17′W, 2,720 m, *Holm-Nielsen et al. 2720* (F, MO); near Montalvo, ca. 40 km E of Babahoyo, foothills of the Andes, 100–200 m, 1°47′S, 79°17′W, *Holm-Nielsen et al. 2720* (AAU, B). MANABI: 11 km E of San Plácido, on road Portoviejo–Pichincha, 400 m, *Harling & Andersson 24978* (F). PICHINCHA: Km 170–175, via Sto. Domingo–Quinindó, 300 m, *Acosta S. 13815* (F); Reserva ENDESA, Carretera Quito–Puerto Quito, km 113, 00°05′N, 79°02′W, *Argüello 498* (AAU); Reserva ENDESA, Carretera Quito–Puerto Quito, km 113, 800 m, 00°05′N, 79°02′W, *Ayala 58* (AAU); San José de Toachi, 100 km W of Quito, 1,000 m, *Bell 200* (BM, GH, S); by Río Toachi, above confluence with Río Pilaton, 1,000 m, *Bell 238* (BM, GH, S); 20 km W of Sto. Domingo de los Colorados, 300 m, *Cazalet & Pennington 5199* (B, K, UC); 20 km W of Sto. Domingo de los Colorados, 300 m, *Cazalet & Pennington 5224* (UC); Sto. Domingo de los Colorados, *Fagerlind & Wibom 1593* (S); Sto. Domingo de los Colorados, 500 m, *Holdridge 1617* (GH); Finca Carlita, at km 13 on road to Sto. Domingo, 550 m, 00°15′S, 79°14′W, *Holm-Nielsen et al. 7066* (AAU); valle Nanegal, Aug. 1874, *Sodiro 8.74* (K); prope Sto. Domingo, Aug. 1875, *Sodiro 8.75* (K).

Asplenium purpurascens is largely restricted to the western side of the Andes of Ecuador (Map 6). It grows in wet forests from 80 to 1,400 m.

The species is characterized by short-creeping rhizomes, atropurpureous petioles and rachises, and pinnatifid pinnae (Fig. 11A). No other neotropical species of section *Hymenasplenium* has regularly pinnatifid pinnae.

The holotype of *A. purpurascens* was not among the specimens we received on loan from B. There were two very small fragments on a sheet at B, but these were not enough to identify the species. We feel confident that we are applying the name correctly because it is possible to distinguish the species based on Mettenius's original description. According to his description, *A. purpurascens* has creeping rhizomes, lustrous purple petioles, and pinnatisect pinnae. The provenance of the type also agrees with applying the name to the above-cited plants.

7. Asplenium repandulum Kunze, Linnaea 9: 65. 1834. TYPE: Peru. Huánuco: Pampayaco, in sylvis montosis ad arborum truncos, July 1829, *Poeppig s.n.* (holotype, B not seen; isotype, NY (fragment) not seen). Figure 12; Map 7.

Plants epiphytic; roots 0.6–1.5 mm wide; rhizome 2.5–7 mm wide, nearly naked; scales 0.5–2.5 × 0.2–0.5 mm, black, ovate-lanceolate, clathrate; petiole base 2.5–4 mm wide, swollen, 1–2 cm distant from each other on the same row; petiole 4–15 × 0.15–0.3 cm, about ⅐–⅓ the leaf length, dark green-brown, fleshy and dull, terete, glabrous; lamina 22–40 cm long, dull green, 1-pinnate, lanceolate to oblong with subconform apex; rachis like petiole, with adaxial green wings in the same plane as the lamina, strongly carinate abaxially; lateral pinnae 4–6 × 1.1–1.8 cm in the middle of the leaf, 12–17 pairs, obliquely oblong to oblong-lanceolate, margin almost entire to only slightly toothed, the basal basiscopic side excavate for ⅐–¼ the pinna length, acute at apex, broadly cuneate and almost sessile at base, auricle 2–6 mm long; veins 1-forked; sori 4–10 mm long; spores 40–48 μm, 64 per sporangium, spiny.

Additional specimens examined. ECUADOR. MORONA-SANTIAGO: Macuma, on the Macuma River, S of Chiquaza, 700 m, *van der Werff 660* (GH, MO). PASTAZA: Baños—aut Jivaria de Pintuc, excurs. nach Canelos, 1,200–1,300 m, *Stübel 878* (B). PICHINCHA: prope Sto. Domingo, Aug. 1875, *Sodiro s.n.* (K). PERU. AMAZONAS: ca. 12 km E of La Peca, Serranía de Bagua, 1,650–1,800 m, *Gentry et al. 23073* (MO, UC). HUANUCO: Leoncio Prado, Dtto. Hermilio Valdizan, road from Pumaguasi to La Cumbre, La Divisoria, 1,600 m, *Plowman & Schunke V. 7363* (F). JUNIN: Chanchamayo, Chanchamayo Valley, 1924–1927, *C. Schunke 155* (F), *897* (F), *907* (F); above San Ramón, Schunke Hacienda, 1,400–1,700 m, *Killip & Smith 24547* (NY), *24804* (NY); Pichita Caluga, 1,800 m, *Walden 41* (BM); Tarma, Chanchamayo Valley, above La Merced at Cumbre Yacunay

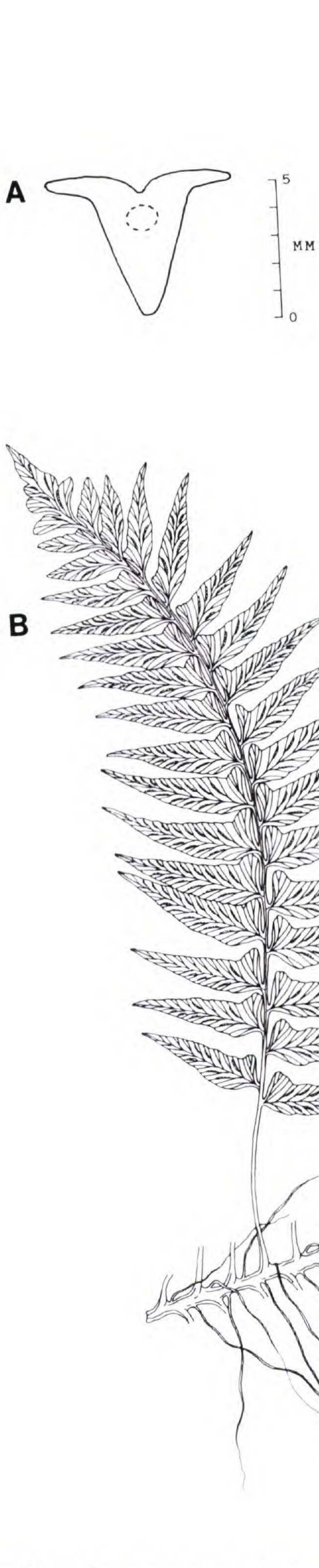


FIGURE 12. *Asplenium repandulum*. —A, B. Ecuador, *van der Werff 660* (MO). Cross section of rachis shown in A.—C. Peru, *Hutchison 1196* (G).

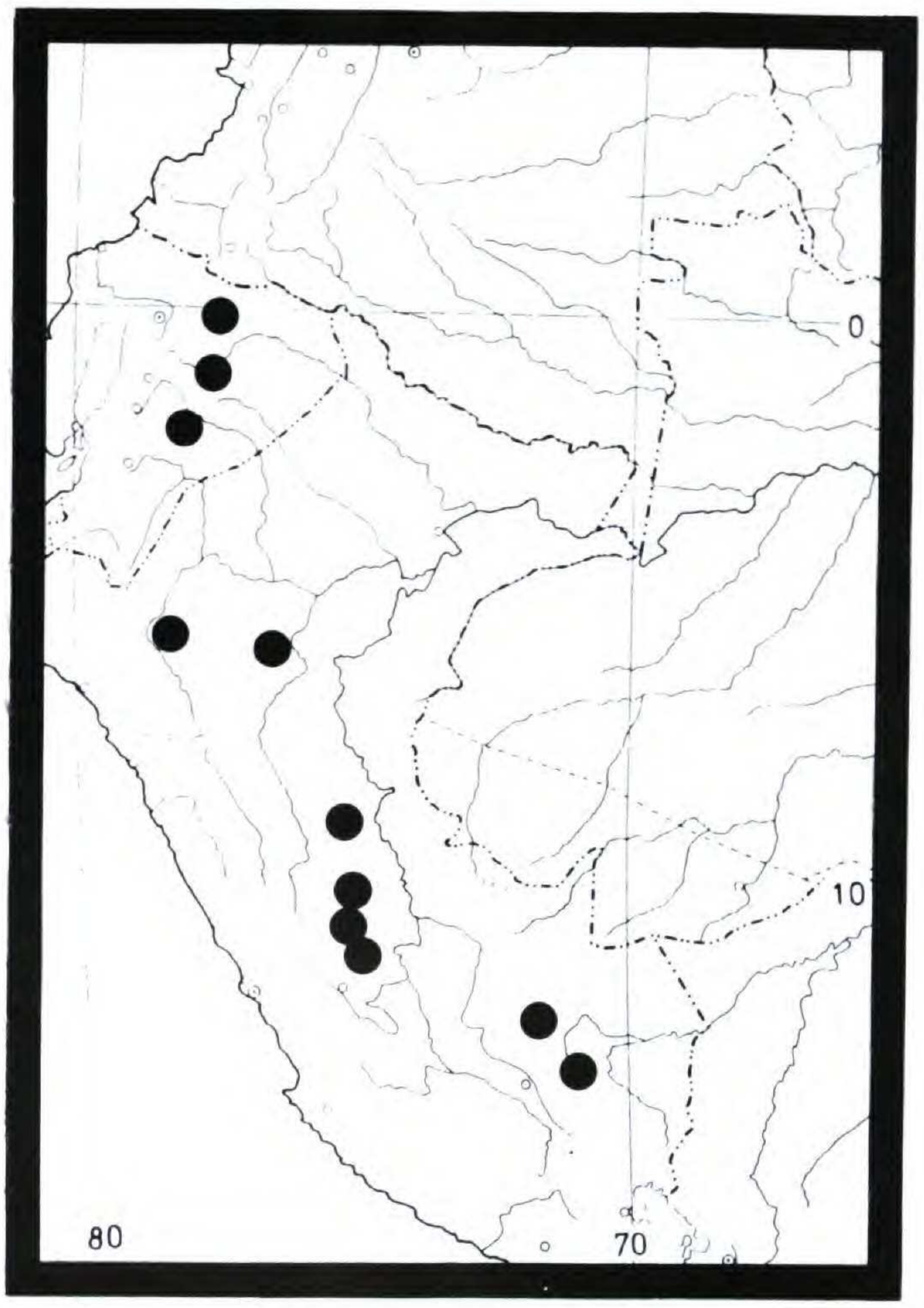
near summit, 2,000 m, *Hutchison 1196* (F, G, M, MICH, MO, NY, S). MADRE DE DIOS: Manú, Parque Nacional de Manú, between Panagua and Tayakome, Cocha Cashu, vicinity of ox-bow lake of Río Manú, *Foster et al. 3449* (F); reise von Moyabomba zum Huallaga, bei Lamas, *Stübel 1099a* (B). PASCO: Oxapampa, vic. of Chequitavo, Gran Pajonal, 1,250 m, 10°45′S, 74°23′W, *D. N. Smith 5168* (MO).

Asplenium repandulum is characterized by long-creeping rhizomes, prominently carinate rachises, and orientation of the rachidial wings in the same plane as the lamina (Fig. 12). It occurs east of the Andes in Ecuador and Peru (Map 7). It grows in wet forests from 700 to 2,000 m as an epiphyte on large tree trunks. One specimen from French Guiana, disjunct from the Andean populations, has a carinate rachis and may represent *A. repandulum* but was collected on wet soil (Sommet Tabulaire, ca. 50 km SE of Saul, 750 m, *de Granville 3508* (F)). In the carinate rachis, it also resembles *A. triquetrum*, but the main range of that species is even farther away than that of *A. repandulum*. It is not typical of either species to grow on the soil. The identity of the plant from French Guiana needs more research.

As outlined in the key, the rachis cross section and orientation of the adaxial wings on the rachis are important taxonomic characteristics distinguishing *A. repandulum*, *A. triquetrum*, *A. riparium*, and *A. volubile*. The characteristics, however, can be difficult to interpret because of changes during pressing and drying. Although the carinate rachis of *A. repandulum* and *A. triquetrum* is a prominent and striking feature of living plants, in pressed plants the keeled edge of the rachis is pushed to one side, so that only one side of the 3-angled rachis faces up. This gives the impression when viewed from above that the rachis is smooth or rounded. When this distortion occurs, it can usually be detected because pinna bases on one side of the rachis are hidden beneath the keel, but the attachments of the pinna bases on the other side are visible.

The orientation of the rachidial wings may be difficult to determine because the wings sometimes shrivel upon drying and (in *A. riparium* and *A. volubile*) the wings may be pressed flat into the same plane of the lamina. Usually, the best place to observe the orientation of the wings is at the pinna junctures.

Asplenium repandulum is most closely related to *A. triquetrum* based on rachidial wing orientation and the strongly carinate rachis. However, *A. repandulum* resembles *A. volubile* by the long-creeping rhizomes and epiphytic habit (see *A. volubile* for comparison).



MAP 7. The distribution of *Asplenium repandulum*.

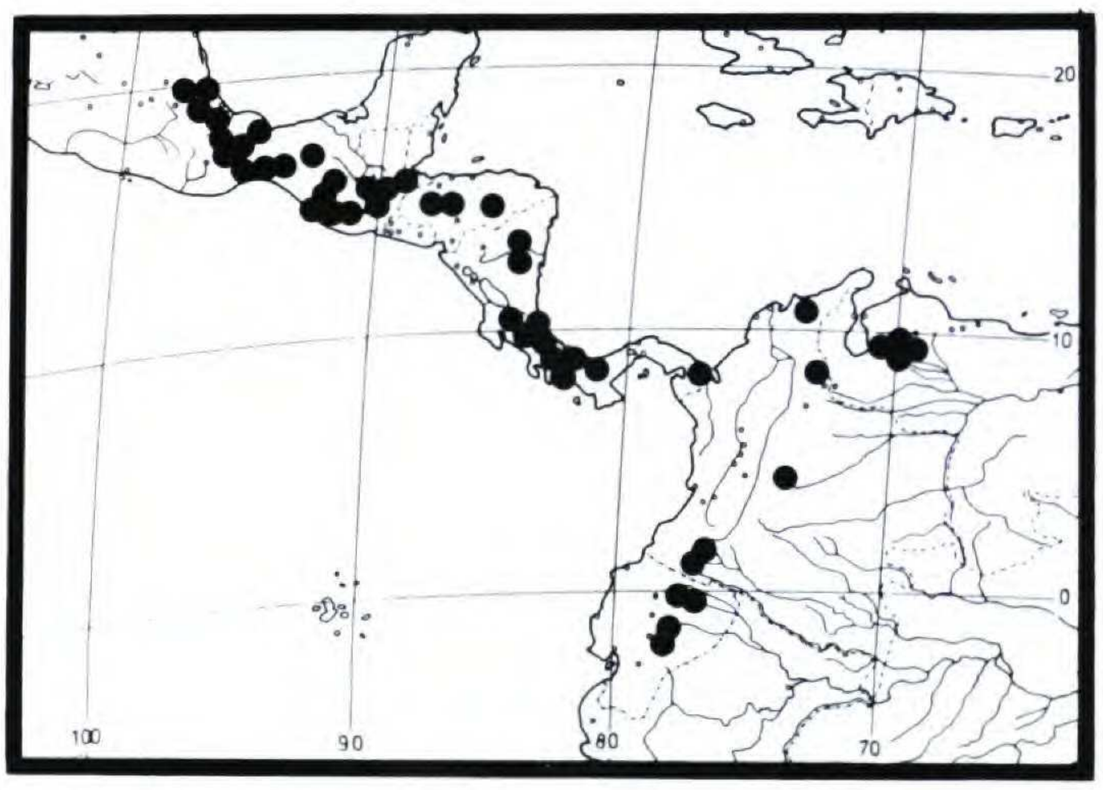
Although we have not seen the holotype of *A. repandulum*, we feel confident that we are applying the name correctly because this is the only epiphytic species of section *Hymenasplenium* that occurs in Amazonian Peru.

8. Asplenium riparium Liebm., Mexic. bregn. 244 (seors. 92). 1849. [= Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 5, 1: 244. 1849]. *Asplenium obtusifolium* L. var. *riparium* (Liebm.) Domin, Pteridophyta Isl. Dominica in Rozpr. Král. Ceské Spolecn. Nauk, Tr. Mat.-Prir., Nov. Rad. 2: 175. 1929. LECTOTYPE (designated by A. R. Smith, 1981): Mexico. Veracruz: Hacienda de Java, *Liebmann* [Fl. Mex. 310] (lectotype, C not seen; isolectotypes, B, K). Figure 13B; Map 8.

Plants epilithic or terrestrial; roots 0.7–1.3 mm wide; rhizome 3–6 mm wide, nearly naked; scales 0.8–1.5 × 0.2–0.4 mm, brown, ovate-lanceolate; petiole base 2.5–4.5 mm wide, swollen, 1–2.5 mm distant from each other on the same row; petiole 10–20 × 0.1–0.25 cm, ⅓–½ the leaf length, dark green-brown, fleshy and dull, broadly and shallowly grooved, glabrous; lamina 15–30 cm long, dark green, 1(–2)-pinnate, lanceolate with conform

FIGURE 13. A–D. *A. riparium.*—A. Cross section of rachis.—B. Fertile leaf, Colombia, *H. H. Smith 968* (MO).—C. Senescent leaf with plantlets, *Murakami s.n.* (MO).—D. Plantlets proliferating from receptacular tissue of senesced leaf.—E. *Asplenium volubile*, Ecuador, *Asplund 5550* (F).

terminal pinna, herbaceous; rachis like petiole, with green wings perpendicular to the plane of the lamina; lateral pinnae 4–8 × 1–2 cm in the middle of the leaf, 8–14 pairs, oblong-lanceolate, the margin toothed, the teeth about 0.5 mm deep, the basiscopic margin excavate for ⅙–⅓ the pinna length, broadly cuneate and almost sessile at base, auricle 1–4 mm long; veins 1–3 times forked; sori 5.5–10 mm long; spores 38–43 μm, 64 per sporangium, spiny. n = 39 or 40 (Smith & Mickel, 1977).



MAP 8. The distribution of *Asplenium riparium*.

Additional specimens examined. MEXICO. CHIAPAS: Mpio. of Rayón, in the Selva Negra 10 km above Rayón Mezcalapa along road to Jitotol, 1,700 m, *Breedlove 26082* (F, MICH, MO, NY), *29819* (F, MICH, NY), *32617* (MICH, NY); Mpio. of Rayón, above Rayón Mezcalapa along road to Jitotol, 1,700 m, *Breedlove 35410* (MO); Mpio. of Cintalapa, 3 km E of Francisco Madero, NE of Cintalapa, 1,250 m, *Breedlove 38081* (MO); 2 mi. N of Colonia Toquian, on S slope of Volcán Tacaná, 1,700 m, *Croat 47151* (MO); in 1864–1870, *Ghiesbreght 416* (K); 11.6 mi. N of Linda Vista Tropical Biol. Sta., Pueblo Nuevo Solistahuacán, *Gittins 4220* (NY); Siltepec, *Matuda 221* (MICH, MO); *Bourgeau 362* (B). OAXACA: Dtto. Villa Alta, from Yetzelalag toward Lovani, 1,200 m, *Hallberg 1498* (NY); Dtto. Tehuantepec, between La Chiguzhe and Guevea de Humboldt, along Continental Divide, 1,100–1,500 m, *Hallberg 1744* (NY, UC); Mpio. Sta. María Chimalapa, ca. 7 km S de Sta. María, por la vereda a la cabecera del Río Escolapa, 400 m, 16°51′N, 94°41′W, *Hernández G. 2457* (NY); ca. 15 km al ESE de Sta. María, filo entre Arroyo Majipana (al O) y Río Blanco (al E), 810 m, 16°52′N, 94°34′30″W, *Hernández G. 2523* (NY); Mpio. Sta. María Chimalapa, ca. 8 km al N de Sta. María, cañada al O de la vereda al paso Jugcuypac del Río Verde, 300 m, 16°57′N, 94°41′W, *Hernández G. & González L. 1749* (MO, NY); 24 km S of Valle Nacional (km 85), road from Ixtlán to Tuxtepec, 900 m, *Mickel 1434* (MICH, NY); Dtto. Ixtlán, 79 km W of Ixtlán de Juárez on Rte. 175, 1 km S of Campamento Vista Hermosa, 1,500 m, *Mickel 5650* (NY, UC); Dtto. Tuxtepec, 4–9 km S of Valle Nacional on Rte. 175, 300–700 m, *Mickel 5893* (UC); 200–700 m, *Mickel 5918* (NY, UC); Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, 500–700 m, *Mickel 6360* (NY, UC); Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, trail E of Rte. 175 at Campamento Vista Hermosa toward Ladú, 500 m, *Mickel 6446* (NY); Dtto. Ixtlán, 7 km S of Vista Hermosa, 71 km N of Ixtlán de Juárez on Rte. 175, 1,800 m, *Mickel 6715* (NY, UC); Dtto. Ixtlán, 2–3 km S of Vista Hermosa, 75–76 km N of Ixtlán de Juárez on Rte. 175, 1,400 m, *Mickel & Pardue 6548* (AAU, NY); Dtto. Ixtlán, 2–3 km S of Vista Hermosa, 75–76 km N of Ixtlán de Juárez on Rte. 175, 1,700 m, *Mickel & Pardue 6580* (UC); Ixtlán, 76 km N of Ixtlán de Juárez on Rte. 175, Campamento La Esperanza, *Mickel 7172* (Z); Villa Alta, ca. 20 mi. NE of Villa Alta, valley of the Yelagago River, 1,200 m, 17°25′N, 96°05′W, *Mickel 1087* (MICH). PUEBLA: Curva de los Millones, 10 km E de Teziutlán, *Riba et al. 318* (NY). VERACRUZ: 8 km S of Misantla, 750 km, *Barrington 404* (GH); 12 km S of Misantla, 1,350 m, *Bohs et al. 1701* (GH); 15 km S of Misantla, Paz de Enriquez cloud forest, *Bohs et al. 1832* (GH); vallée de Córdoba, *Bourgeau 2014* (B, GH, K, L, MICH, MO, NY); 8 km S of Misantla, 750 m, *Conant 700* (GH); in 1889–1891, *Finck 35* (NY); Mirador, *Galeotti 6274* (BR, K), *6275* (photo GH ex BR), *Linden 31* (MICH); Sta. Rita prope Misantla, *Hahn 362* (K); 12 km S of Misantla, 1,350 m, *Kress et al. 703* (GH); Barranca de Mirador, *Liebmann s.n.* (B, K); Mirador, in 1839, *Linden 68* (K); Orizaba, in 1835, *Müller 1772* (NY); 7.2 km E of Tebanca, 7.2 km E of E side of Lago Catemaco, 2.6 km W of Bastonal lumber camp, 910 m, *Nee & Schatz 19943* (F); Barranca of Texolo, near Jalapa, 1,100 m, *Pringle 7889* (GH); Zacuapan, *Purpus 1983* (B, UC); Barranca de Tenampa, *Purpus 2846* (B, BM, F, GH, MO), *Purpus 2946* (M), *Purpus 15420* (F); environs of Xalapa, road from Xalapa to Misantla, Paz de Enriquez, N of Naolinco, 1,600 m, *Sperling 4945* (GH); below Sta. Rita, 12 km S of Misantla, 1,350 m, *Sperling 4995* (GH); Mpio. Yecuatla, Loma Santa Rita, 1,300 m, *Ventura A. 3267* (NY); Mpio. de Atzalan, Ranchito El Caballo, 1,000 m, *Ventura A. 14368* (G); Mpio. Totutla, El Mirador, 1,000 m, *Ventura A. 16002* (MO). GUATEMALA. ALTA VERAPAZ: trail between Sepacuite and Secanquim, 1,000 m, *Maxon & Hay 3263* (BM, F, NY); E of Tactic, on road to Tamahú, 1,500–1,650 m, *Standley 71321* (F); road between Tactic and the divide on road to Tamahú, 1,500–1,600 m, *Standley 90658* (F); between Tactic and the divide to Tamahú, 1,500–1,600 m, *Standley 90667* (F, UC); Pansamalá, 1,200 m, *von Türckheim 630* (B, GH, K, NY, UC). BAJA VERAPAZ: San Rafael Chilasco, Salama, *Guzmán V. 553* (F); Los Andes, Finca Panama, *Brenckle 47-201* (UC). IZABAL: Cerro San Gil, 300–900 m, *Steyermark 41908* (F). QUEZALTENANGO: Volcán Zunil, 1,500 m, *Skutch 976* (GH); Finca Pirineos, below Santa María de Jesús, 1,350–1,380 m, *Standley 68216* (F); road between Finca Pirineos and Patzulín, 1,200–1,400 m, *Standley 86710* (F); between Finca Pirineos and Patzulín, 1,200–1,400 m, *Standley 86744* (F, UC). SAN MARCOS: Barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta, in upper part of the barranco between Finca La Lucha and Buena Vista, 2,500–2,700 m, *Standley 86332* (F). HONDURAS. COMAYAGUA: ca. 8 km SW of Siguatepeque, road to Jesús de Otoro, 1,200 m, *Burch 6114* (NY); near El Rincón, *Clewell 3097* (NY); Cerro Azul-Meambar, 1,100 m, *Horwath 72* (F), *74* (F). OLANCHO: 8.5 km W de Catacamas, márgenes del Río del Real, 900 m, *Ortega U. 295* (MO). PROV. UNKNOWN: Mr. Elliot's plantation, *Wilson 37* (NY). NICARAGUA. ZELAYA: Costado sur del Cerro La Pimienta, y N del Cerro

El Hormiguero, a orilla del Caño El Hormiguero, 800–900 m, 13°44′45″N, 84°59′45″W, *Grijalva 299* (UC); Costado SW de Cerro El Hormiguero, 900–1,000 m, 13°44′10″N, 84°59′50″W, *Grijalva 471* (UC); Cerro Saslaya, 1,100 m, *Neill 3820* (MO); Caño El Hormiguero, 750–800 m, 13°46′N, 84°59′W, *Pipoly 5929* (MO); trail toward Cerro El Inocente to Cerro Saslaya, 1,050–1,150 m, 13°46′N, 85°01′W, *Stevens 6677* (MO). COSTA RICA. ALAJUELA: near Cariblanco, along road to Colonia Virgen del Socorro, 800 m, *Burger et al. 11916* (F); forest along Río Sarapiquí upstream from crossing of road to Colonia Virgen del Socorro, 740 m, *Grayum & Hammel 5530* (CR, F, GH, MO); Reserva Forestal San Ramón, *Hernández 8608* (CR); Reserva Forestal de San Ramón, Río San Lorenzito, agua arriba a partir de la estación, 800–1,000 m, 10°12′53″N, 84°36′28″W, *Herrera Ch. et al. 339* (MO, UC), *Moran 4119* (CR, F, MO, UC), *Moran 4136* (CR, MO, UC); ca. 23 km NE of San Ramón, along Río La Balsa, 850 m, *Taylor 17819* (NY). CARTAGO: hills at N side of Río Navarro, between Río Sombrero and Quebrada Solon, W of El Muñeco, 1,260–1,400 m, 9°55′N, 83°48′W, *Grayum & Hammel 8466* (CR, MO, UC); E of Turrialba, road to Siquirres between Sabillas and Chitaría, ca. 1 km NE of Finca Mata de Caña, 900 m, *Lellinger & White 1431* (F, MO); 3 km SE of Cachí, 1,420 m, *Lent 2063* (CR, F); 22 km E of Turrialba, high ridge above Platanillo, 1,200–1,450 m, *Mickel 3401* (NY); 1 km E from Buenavista, 20 km NE of Turrialba, Río Chitaría, 750 m, *Saiki CR-59* (F); El Muñeco, 900 m, *Stork 2678* (UC). GUANACASTE: región del Volcán Cacao, Rancho Herold, 700–1,200 m, *Chacón & Chacón 2115* (CR). HEREDIA: OTS Field Station, banks of Quebrada El Saltito, 100 m, *Folsom 9735* (F, MO); Cacho Negro, Alto de los Quetzales, 1,700 m, *Gómez 2168* (F, GH, NY); Atlantic slope of Volcán Barva, along W fork of Río Sardinal, near future site of Rara Avis and to ca. 0.5 km upstream therefrom, 670–720 m, 10°17′N, 84°03′W, *Grayum 8506* (MO); Zona Protectora, between Río Peje and Río Guácimo, N slopes of Volcán Barba, 280 m, *Grayum & Schatz 3140* (CR); 9 km SW of Las Horquetas, between Quebrada Tigre and E fork of Río Sardinal, 600 m, *Grayum et al. 5060* (MO). LIMON: Hitoy Cerere reserve, SW of Valle La Estrella, ridge between Río Cerere and Quebrada Barrera, 150–550 m, 9°39′N, 83°02′W, *Grayum et al. 5808* (CR, MO, UC); Toro Amarillo, Guápiles, 350 m, *Lent 330* (GH); SE of Siquirres, Alto Guayacá, *Lent 1411* (F); Cantón de Talamanca, Croriña, Cerro Cruibeta, afluente de Quebrada Lumbeta, 9°25′15″N, 82°59′00″W, 550 m, *Herrera 3311* (MO, UC); SW of Guápiles, W side of Río Toro Amarillo, 1,000 m, *Rossbach 3860* (GH); Siquirres, 60 m, *Kupper 545* (M); Suerre, llanuras de Santa Clara, 300 m, *J. D. Smith 6885* (B, BM, F, G, GH, M, NY); Talamanca, forets de Tsâki, 200 m, *Tonduz 9473* (CR); 1901–1905, *Wercklé 1713* (NY, S). PUNTARENAS: Cordillera de Talamanca, area around Río Canasta, 9.5 km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, 1,500–1,600 m, 9°02′N, 82°59′W, *Davidse et al. 28440* (AAU, CR, MO, UC), *28518* (UC); 5 km S of San Vito de Java, vic. of biological field station at Finca Wilson, 1,100–1,200 m, *Mickel 3143* (NY); Monteverde, 1,100 m, *Palmer 117* (NY). SAN JOSE: Tablazo, 1,900 m, *Brade 765* (B, M, NY, S, UC); Carillo, 400 m, *Kupper 528* (M); vic. of El General, 975 m, *Skutch 2715* (GH, MICH, MO, NY, S); 35 mi. S of Cartago, 5 mi. S of Santa María de Dota, 1,300 m, *Stork 1767* (GH, MICH, UC). PANAMA. CHIRIQUI: near Fortuna Dam, 1,200 m, *Hampshire & Whitefoord 212* (BM); ca. 3.5 km NW of Bajo Mono, along Río Caldera (Boquete region) and on slope to the east, 1,600 m, 8°50′N, 82°28′W, *Smith et al. 2455* (UC); no locality given, *Wagner 809* (M); Dtto. Boquete, Fortuna Dam site, Continental Divide, 1,100 m, *van der Werff & van Hardeveld 6766* (MO, UC). DARIEN: Serranía del Darién, Cerro Tacarcuna, 1,550–1,650 m, *Gentry 14069* (MO). PANAMA: Above Sta. Fé, beyond Escuela Agrícola, 1.8 mi. beyond fork in road on Pacific slope, *Croat 34167* (MO). VERAGUAS: Valley of Río Dos Bocas, road between Alto Piedra (above Sta. Fé) and Calovebora, 350–400 m, *Croat 27417* (MO). VENEZUELA. BARINAS: Dtto. Bolívar, entre Sto. Domingo y Altamira, en el sitio denominado Quebradón, en el camino que lleva al tunel que va hacia la represa, 1,300–1,500 m, *Ortega & van der Werff 2355* (MO, UC). MERIDA: Mérida, *Engel s.n.* (B). PORTUGUESA: Dtto. Sucre, Los Paramitos, 20 km por aire al SO de Biscucuy, 1,000–1,500 m, 9°20′N, 69°05′W, *Ortega et al. 1824* (MO, NY, UC); Dtto. Guanare, ESE of Paraíso de Chabasquén, along road to Córdoba, ca. 27 min. from Chabasquén, just below summit and below road, 1,500 m, 9°23′N, 69°54′W, *A. R. Smith et al. 1037* (MO, UC, Z). TRUJILLO: Dtto. Boconó, 33.5 km SE of Boconó, road to Guaramacál, 1,300 m, 9°12′N, 70°06′W, *A. R. Smith et al. 1545* (MO, UC). COLOMBIA. CUNDINAMARCA: Salto de Tequendamama, 2,300 m, *Cuatrecasas 194* (F). HUILA: Guadalupe, carretera vía a Florencia, a 2 km, 1,100 m, *Osorio 112* (COL). MAGDALENA: Santa Marta, above Onaca, 1,100 m, *H. H. Smith 968* (BM, F, GH, L, MICH, MO, S, UC). NARINO: Mpio. Ricuarte, along Río Imbí, 2–3 km above Ecopetrol Campamento Palmar, 3 km W of Ricuarte, 1,150 m, *Croat 71551* (MO); Ricuarte, entre Arrayán y Las Vegas, 1,400 m, *Mora 4087* (COL). SANTANDER: *Kalbreyer 857a* (B). TOLIMA: Casas de las Varones, *Stubel 16a* (B). ECUADOR. NAPO: Cascada San Rafael, km 101 via Lago Agrío, falls on Río Quijos, 1,275–1,375 m, *Foster 85-150* (UC); Archidona, Carretera Hollin–Loreto, Río Huataraco, 800–1,000 m, *Cerón & Factos 7450* (MO, QCNE). PASTAZA: Colonia Játiva ca. 7 km N of Mera, 1,200–1,300 m, *Harling & Andersson 16908* (AAU, F, MO); 2 km al NE de Mera, Hacienda San Antonio del Barón von Humboldt, 1,300 m, *Baker et al. 5797* (MO).

Asplenium riparium grows on boulders along streams in wet forests from 200 to 1,900(–2,300) m. It ranges from Mexico to western Venezuela, Colombia, and Ecuador (Map 8).

The species is characterized by short-creeping rhizomes, petioles ⅓–½ the length of the lamina, and abaxially rounded (not carinate) rachises (Fig. 13A).

Since Liebmann's publication of *Asplenium riparium*, almost all pteridologists have considered it synonymous with *A. repandulum*. The two species clearly differ, however, by the rachidial characteristics used to separate them in the key. In addition, they differ in habitat: *A. riparium* grows on boulders along streams, while *A. repandulum* grows on tree trunks. The two species overlap in range only in eastern Ecuador (Maps 7, 8).

Asplenium riparium is most closely related to *A. volubile* because both have strongly carinate

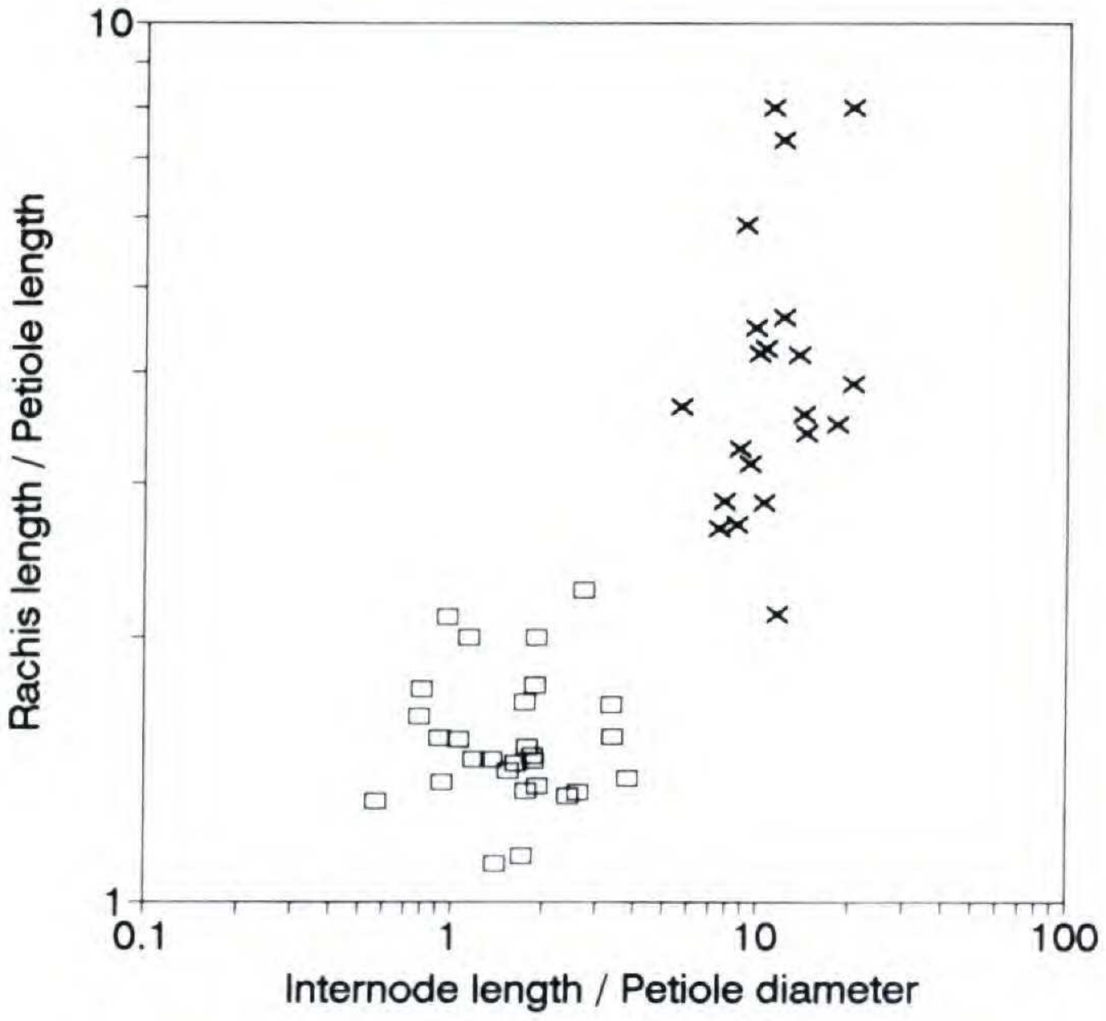


FIGURE 14. Quantitative differences between *A. riparium* (open squares) and *A. volubile* (X). The measurements were taken from herbarium specimens throughout the entire range of both species.

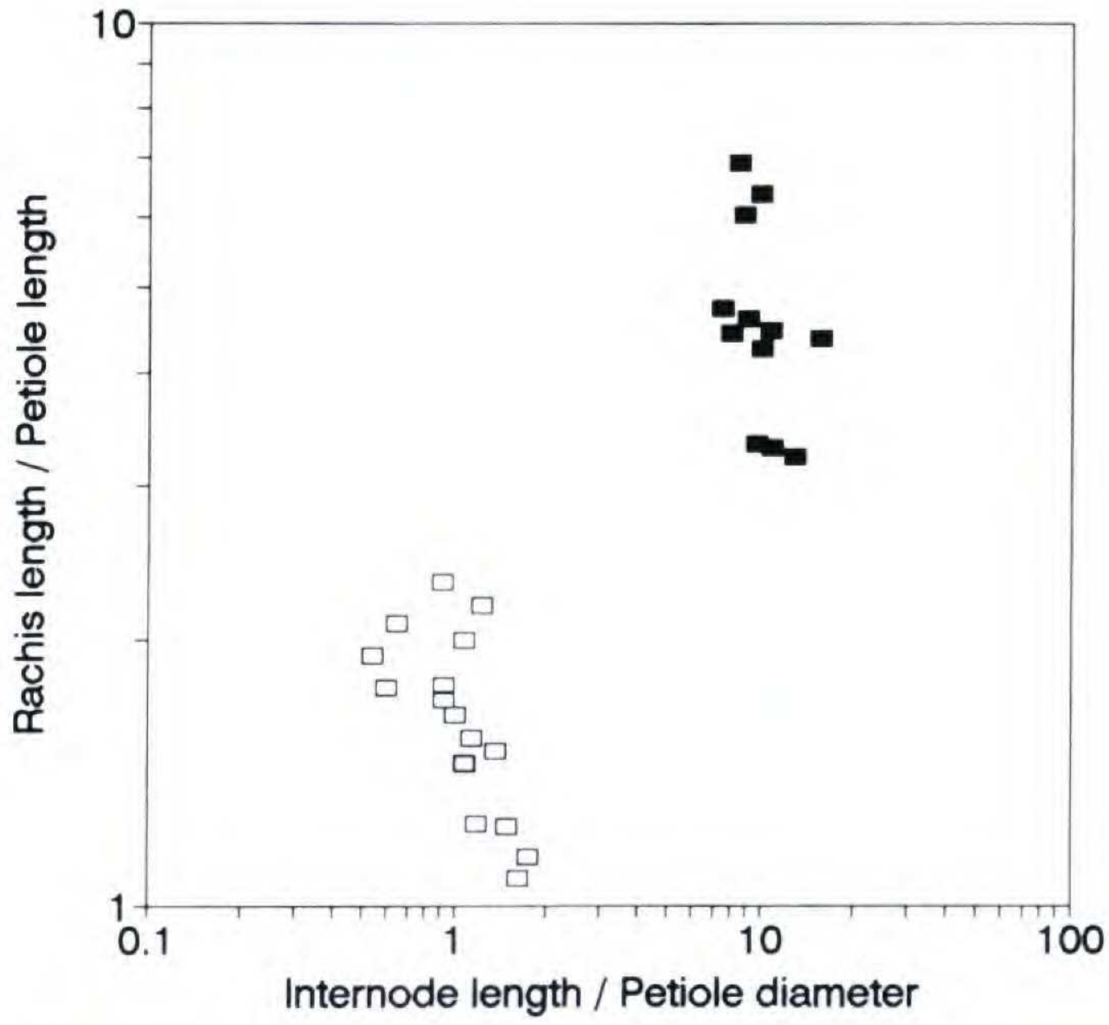


FIGURE 15. Variation in quantitative characteristics of *Asplenium riparium* (open squares) and *A. volubile* (black squares) from the Fortuna Dam area, Panama. The measurements were taken from living plants.

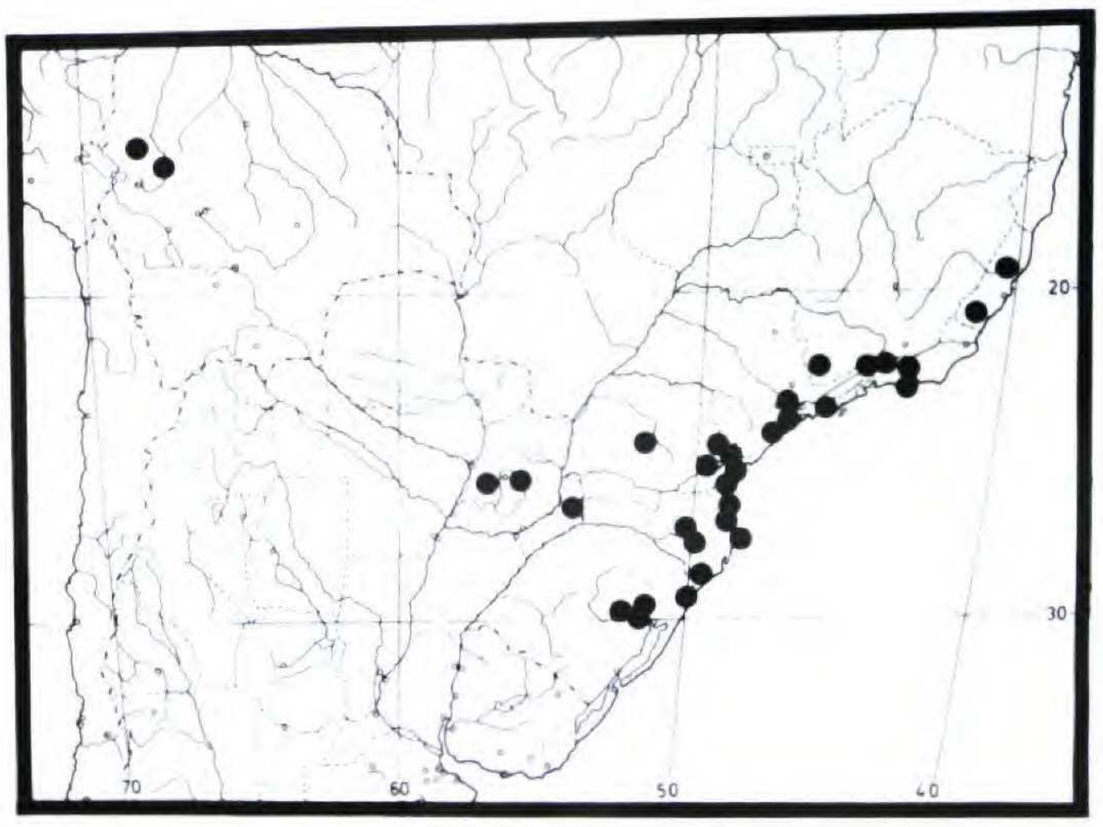
rachises. The two species are easily distinguished by the features given in the key. Petiole length relative to the lamina and internode distance clearly distinguish the two species (Fig. 14). Figure 15 shows that the two species maintain their distinctive characteristics even when growing in the same population.

The most remarkable thing about *A. riparium* is that it produces plantlets from the soral receptacles on senescent leaves that have drooped and touched the soil (Fig. 13C, D). Iwatsuki & Kato (1985) and Kato & Iwatsuki (1985) mentioned that several Old World species of section *Hymenasplenium* produce plantlets on the pinnae, but they did not specify whether the plantlets proliferated from the soral receptacles.

9. Asplenium triquetrum Murakami & R. C. Moran, sp. nov. TYPE: Bolivia. La Paz: Prov. Nor Yungas, Polo-Polo bei Coroico, 1,100 m, *Buchtien 625* (holotype, MO; isotypes, BM, K, NY, Z). Figure 8B, C; Map 9.

Plantae terrestres; rhizoma 2–6 mm latum, fere nudum, breviter reptans, internodis 0.4–2 cm longis; squamae 1–2.3 × 0.5–1.2 mm, ovatae, clathratae; laminae 22–40 cm longae, 1-pinnatae, 12–17 jugatae, lanceolatae vel oblongae, apice subconforme; rhachis triquetra, alis viridibus, ad laminam parallelis; pinnae 5–9 × 1.1–1.8 cm; venae 1–3 furcatae; sori 5–9 mm longi; sporae spinosae.

Plants terrestrial; roots 0.4–1.2 mm wide; rhizome 2–6 mm wide, nearly naked; scales 1–2.3 × 0.5–1.2 mm, dark brown, ovate, clathrate; petiole base 2–4 mm wide, swollen, 0.4–2 cm distant from each other on the same row; petiole 10–25 × 0.15–0.25 cm, ⅓–½ the leaf length, dark green-brown, fleshy and dull, glabrous, shallowly grooved; lamina 22–40 cm long, dark green, 1-pinnate, lanceolate to oblong with subconform apex; rachis with abaxial green wings in the same plane as the lamina, strongly carinate abaxially; lateral pinnae 5–9 × 1.1–1.8 cm in the middle of the leaf, 12–17 pairs, obliquely oblong to oblong-lanceolate, the margin occasionally lobed, almost entire to only slightly toothed, the basiscopic margin excavate for ⅐–⅓ the pinna length, acute at apex, broadly cuneate and almost sessile at base, auricle 2–6 mm long; veins 1–3 times forked; sori 5–9 mm long; spores 40–52 μm, 64 per sporangium, spiny.



MAP 9. The distribution of *Asplenium triquetrum*.

Paratypes. BOLIVIA. LA PAZ: Prov. Larecaja, Mapiri, 650 m, *Tate 401* (NY); 1,100 m, *Buchtien 3348* (GH, S). PARAGUAY. GUAIRA: Cordillera de Ybytyruzú, Cerro Peró, 1 km W of Destacamento Tororo, *Zardini 10966* (MO); Cerro Peró, 1 km W of Destacamento Tororo, around cave, 500 m, *Zardini & Aguayo 9501* (MO). PARAGUARI: Parque Nacional Ybycu'í, vecino al Salto Guaraní, *Aguayo 268* (MO). BRAZIL. PROV. UNKNOWN: *Glaziou 7247* (B); *Glaziou 7954* (B); *Glaziou 12283* (B); no locality, *Martius 342* (BM, L); São Pedro, Montenegro, 400 m, *Sehnem 2977* (B); Pinhal, Montenegro, 500 m, *Sehnem 6501* (B); Itajahy, *Ule 70* (B). ESPIRITO SANTO: Serra Tiutobá, Rio Docc., *Luetzelburg 7150b* (M, S). MINAS GERAIS: Caldas, *Mosen 2111* (GH). PARANA: Serra do Mar, inter Ypiranga ab Volta Grande, 600 m, *Dusén 3351* (MO, S); Ypiranga, *Dusén 3551* (S); Serra do Mar, Desvio Ypiranga, 700 m, *Dusén 6774* (G, S); Guaratuba, *Dusén 13730* (S); Serra do Mar, Desvio Ypiranga, 19 Sep. 1908, *Dusén s.n.* (BM, BR, F, G, GH, K, MO, NY, S, Z); Mpio. Morretes, Rio Mas Catira, 100 m, *Hatschbach 23237* (UC); Mpio. Morretes, Estr. Graciesa, Greta Funda, 500 m, *Hatschbach 24738* (MO, S, UC); Mpio. Morretes, Jurape, *Hatschbach 41961* (UC, Z). RIO DE JANEIRO: Organ Mts., 1837, *Gardener 168* (K); environs de Rio de Janeiro, *Glaziou 12289* (K); Sebastianipol, ad rivulos Mandioccae, *Martius s.n.* (B, K, M); Serra d'Estrella, Aug. 1817, *Martius s.n.* (M); Serra dos Orgãos, 1817, *Martius s.n.* (M); near Rio de Janeiro and Bahia, *Webb 66* (NY); Serra Estrella, *Luetzelburg 21* (M); Serra dos Orgãos, Morro Assu, Garganta, *Luetzelburg 6209* (M, S, UC), *Luetzelburg 6296a* (M); Serra Estrella bei Petropolis, wasserfall, 1,800 m, *Luetzelburg 6301* (M, MICH, UC); Serra Estrella, *Luetzelburg 6888* (F, K, M, MICH, UC); Serra Estrella bei Petropolis, *Luetzelburg 7396* (M); Corcovado, waterfall, 600 m, *Luetzelburg 13007* (M); Rio de Janeiro, *Mosén 2665* (B, K, S); Mandioca, *Sellow s.n.* (B). RIO GRANDE DO SUL: Sta. Cruz, Rio Cartichaninho, *Jürgens 372* (B, BM, M, S, UC); Sta. Cruz, Serra de Melo, *Jürgens 391* (S). SANTA CATARINA: Joinville, *Muller 186* (NY); Araranguá, *Reitz 729* (K, MO); Florianopolis, Sertão da Lagoa, *Rohr 1054* (B, L, NY); Pirabeiralea, *Schmalz 81* (S); Joinville, 800 m, *Schmalz 186* (F); Lages, *Spannagel 143* (NY, S, UC); Curitiba, *Viereck 1* (M). SAO PAULO: Iguape, 10 Sep. 1917, *Brade s.n.* (GH); Morro das Pedras, *Brade 5242* (S); Serra da Cantareira, prope São Paulo, 1,100 m, *Brade 6528* (GH); Cajuva, *Brade 8240* (GH, NY); Alto da Serra, *Edwall & Puttemans 5004* (S); *Luederwaldt 21480* (NY); Rio Grande, *Wacket 162a* (UC). ARGENTINA. MISIONES: Cordillera de Misiones, Picada a Carupimas de Américo, Salto del Encuentro, Río Piray, *Niederlein 1922* (B).

Asplenium triquetrum is the southernmost species of the section (Map 9). It grows from 400 to 1,100 m on wet rocks along deeply shaded streambanks, around cave entrances, and near small waterfalls.

Asplenium triquetrum is characterized by its epipetric habitat, strongly carinate rachis, and orientation of the rachidial wings in the same plane as the lamina (Fig. 8B, C). It is most closely related to *A. repandulum* (which see).

10. Asplenium volubile Murakami & R. C. Moran, sp. nov. TYPE: Ecuador. Cotopaxi: Quevedo–Latacunga road, km 46 from Quevedo, 600 m, 0°55′S, 79°11′W, *Holm-Nielsen et al. 2905* (holotype, MO; isotypes, AAU, F, UC). Figure 13E; Map 10.

Plantae epiphyticae; rhizoma 2.5–3.5 mm latum, fere nudum, longe reptans, internodiis 2–4 cm longis; squamae ovato-lanceolatae; laminae 22–35 cm longae, 1-pinnatae, oblongo-lanceolatae vel ovatae, apice conforme vel subconforme; rhachis abaxialiter rotundata, alis viridibus ad laminas perpendicularibus; pinnae 4–5.5 × 0.9–1.7 cm, 11–18 pares; venae 2-furcatae; sori 5–10 mm longi; sporae spinosae.

Plants epiphytic; roots 0.5–1.2 mm wide; rhizome 2.5–3.5 mm wide, nearly naked; scales 1–1.3 × 0.2–0.4 mm, brown, ovate-lanceolate; petiole base 2.2–3.8 mm wide, swollen, 2–4 cm distant from each other on the same row; petiole 4.5–11 × 0.1–0.25 cm, ⅐–¼ the leaf length, dark green-brown, fleshy and dull, shallowly grooved; lamina 22–35 cm long, dark green, 1-pinnate, oblong-lanceolate to ovate with a conform to subconform apex, thin-herbaceous; rachis like petiole, with green wings perpendicular to the plane of the lamina; lateral pinnae 4–5.5 × 0.9–1.7 cm in the middle of the leaf, 11–18 pairs, oblong-lanceolate, the margin only slightly toothed, excavate ⅕–⅓ portion of the basal basiscopic side absent, acute-obtuse at apex, broadly cuneate and almost sessile at base, auricle 1.5–5 mm long; veins 2-forked; sori 5–10 mm long; spores 48–50 μm, 64 per sporangium, spiny.

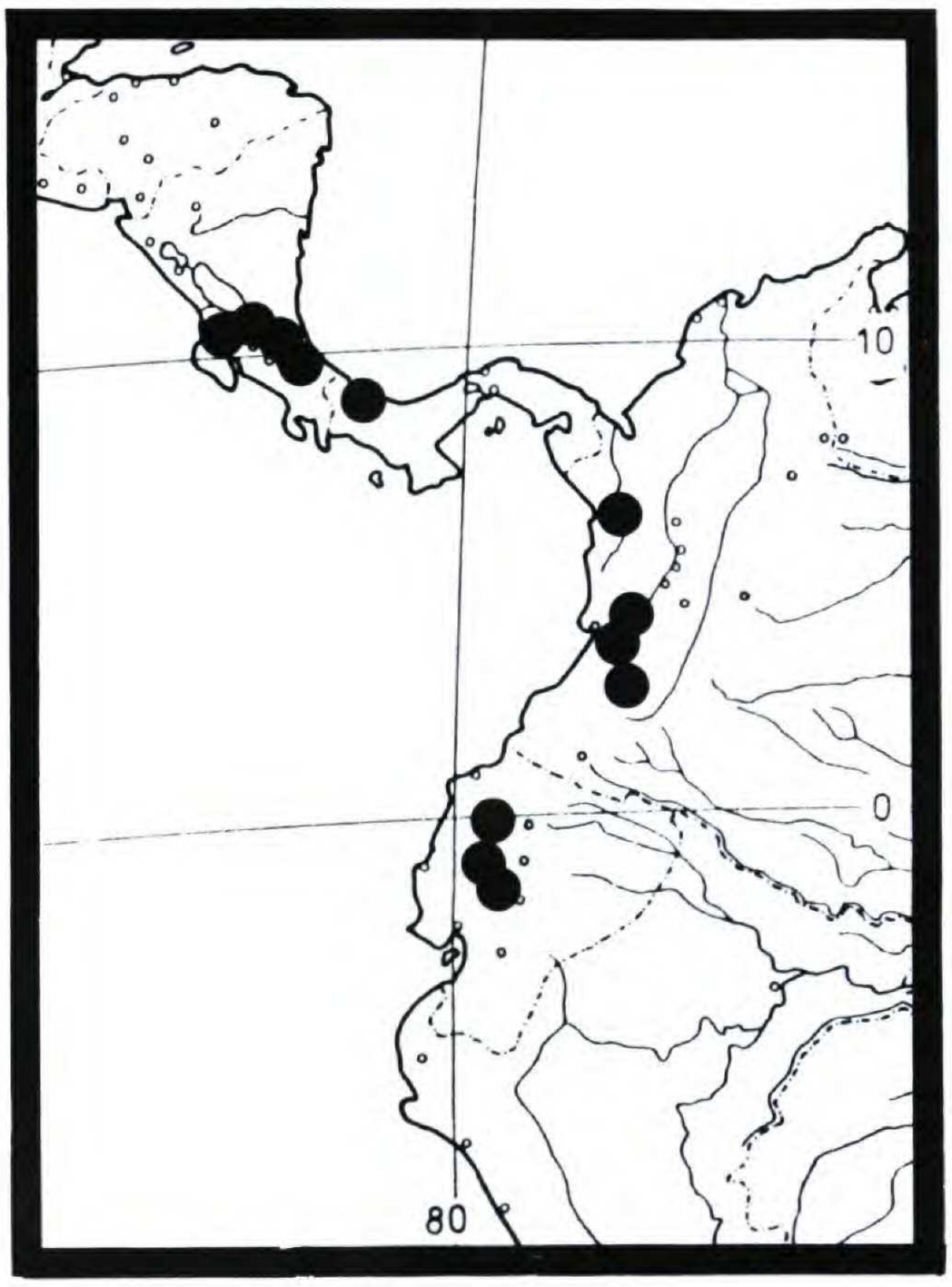
Paratypes. COSTA RICA. ALAJUELA: Upala, Bijagua, El Pilón, Río Celeste, 700 m, 10°49′N, 84°27′W, *Herrera 1248* (CR, F, MO, UC); SW of Cariblanco, between Río Cariblanco and Quebrada Quicuyal, canyon of Río Cariblanco and W slope and summit of ridge, 840–950 m, 10°16′N, 84°12′W, *A. R. Smith et al. 1875* (CR, MO, NY, UC). GUANACASTE: border with Alajuela, above Bijagua, slopes of Miravalles, 1,500 m, *Gómez et al. 19195* (MO, UC). LIMON: 5 km SW de Guápiles, bosque cerca del Río Toro Amarillo, 300–400 m, *Jiménez M. 2816* (CR, F, NY). PANAMA. BOCAS DEL TORO: along Continental Divide from road, branching N off main Fortuna–Chiriquí hwy. near Continental Divide, 1.1 mi. from main hwy., 1,200 m, 8°44′N, 82°17′W, *Croat & Grayum 60307* (MO, UC); 5.3 mi. N of bridge over Fortuna Dam, between Fortuna and Chiriquí Grande, 1.2 mi. N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat & Grayum 60425* (MO). COLOMBIA. CHOCO: San José del Palmar, hoya del Río Torito (afluente del Río Hábita), declive occidental, Finca "Los Guaduales," 630–730 m, *Forero et al. 6840* (COL, MO), *7237* (COL, MO). HUILA: Cordillera Oriental, vertiente occidental, abajo de Gabinete en la hondonada del Abra de San Andrés, 1,900–2,100 m, *Cuatrecasas 8607* (F). VALLE: arriba de La Glorieta, camino a Miralindo, Cordillera Occidental, vertiente oriental, Hoya del Río Cali, vertiente derecha, Quebradahonda, 2,100–2,250 m, *Cuatrecasas 18441* (COL, F, G); El Silencio, Yanaconas, 1,900–2,200 m, *Killip & García 33811* (COL, GH). ECUADOR. COTOPAXI: "Andes Quitensis," Chimborazo, *Spruce 5689* (G, K). LOS RIOS:

Cerro Mombe, Hacienda Clementina on Río Pita, 660 m, *Asplund 5550* (S); Hacienda Clementina, Samana, 750 m, *Harling 552* (S). NAPO: slopes of Guagra Urcu, on the loma above Río Bretania, 200–2,200 m, 0°28′S, 77°45′W, *Holm-Nielsen et al. 26835* (AAU). PICHINCHA: Toachi ad San Miguel, *Sodiro 66* (UC).

Asplenium volubile occurs in Costa Rica, Panama, and coastal Colombia and Ecuador (Map 10). It grows from 300 to 2,200 m in wet forests as an epiphyte on small trees or saplings.

Asplenium volubile has been previously identified as *A. repandulum*. In addition to the rachis characteristics given in the key, it differs from *A. repandulum* by its shorter petiole (4.5–11 cm long), which is only ⅐ to ¼ the leaf length (petiole 10–25 cm long and about ⅓ the leaf length in *A. repandulum*). In both species the rhizome is long-creeping and epiphytic, but field observations by both of us have shown that the rhizomes differ in habit. *Asplenium volubile* has a twining rhizome that grows spirally around the trunks of young trees or saplings that are usually less than 5 cm wide. This characteristic can usually be ascertained in herbarium specimens because the rhizomes appear sinuous or contorted. In contrast, *A. repandulum* grows on large trees and the rhizome is more or less straight, not spiraling upward around the trunk. *Asplenium volubile* has a longer-creeping rhizome than *A. repandulum*. The distance between petiole bases on the same side of the rhizome (orthostichy) is 2.2–3.8 cm in *A. volubile*, and 0.4–2 cm in *A. repandulum*. In addition to the morphological characteristics, the two species differ completely in range: *A. volubile* is restricted to the western side of the Andes (Map 10) and *A. repandulum* is restricted to the eastern side (Map 7).

See *A. riparium* for comparison to that species.



MAP 10. The distribution of *Asplenium volubile*.

HYBRIDS

11. Asplenium ×papyraceum (Jermy & T. Walker) Murakami & R. C. Moran, comb. nov. *Diplazium ×papyraceum* Jermy & T. Walker, Bull. Brit. Mus. (Nat. Hist.), Bot. 13: 264, fig. 10. 1985. TYPE: Trinidad. Charuma Ward: Central Range Forest Reserve, Brickfields Teak Plantation, 3 mi. S of Forest Resthouse, 60 m, in wet ground by stream, 9 July 1963, *Walker T6178* (holotype, BM not seen).

Plants terrestrial; rhizome 2–3 mm wide, sparsely scaly; scales 1–1.5 mm long, narrowly lanceolate, blackish, entire; petiole base 2–3 mm wide, ca. 1 mm distant on the same row; petiole 15–22 cm long, brown, slightly shorter than the lamina, gray-green with narrow black wings, glabrous; lamina 25–30 × 12–17 cm, 1-pinnate, ovate-lanceolate, the apex abruptly to gradually reduced, pinnatifid; rachis brown, sparsely scaly with minute (0.5–1 mm long) filiform, unicostate scales and slightly longer, narrowly triangular scales; pinnae 7–8.5 × 1.5–2.2 cm, short-petiolulate, 9–12 pairs, the basal basiscopic margin slightly excavate, the acroscopic margin coarsely serrate, the serrations 1–2 mm deep; veins 2 or 3 times forked; sori 3–11 mm long; spores abortive.

Specimen examined. TRINIDAD. CHARUMA WARD: Central Range Forest Reserve, Brickfields Teak Plantation, 3 mi. S of Forest Resthouse, 60 m, in wet ground by stream, 9 July 1963, *Jermy 2178* (BM).

Asplenium ×papyraceum is known only from the above-cited locality in Trinidad. Jermy & Walker (1985) have an excellent photograph of the paratype (*Jermy 2178*). The plants resemble *A. delitescens* but differ by their shorter, relatively wider, and more numerous pinnae.

Asplenium ×papyraceum is believed to be a hybrid based on its irregular meiosis, two size classes of chromosomes, triploid chromosome number, and abortive spores (Jermy & Walker, 1985). The asplenioid characteristics of *A. ×papyraceum* are clathrate scales and an X-shaped petiolar strand that unites distally in the petiole. It belongs to section *Hymenasplenium* as evidenced by its short-creeping rhizome with a typical broad ventral meristele and by its rachis-costa structure.

Jermy & Walker (1985) discussed the evidence relating the hybrid to *Asplenium*, but concluded that it belonged in *Diplazium* based on the chromosome count of $n = 123$, a multiple of 41, which is the base number for *Diplazium*. The count of $n = 123$, however, does not exclude *Asplenium*. Although a base number of 41 is not known in *Asplenium*, it is not far off from the numbers known in section *Hymenasplenium*, which have $n = 38$ or 39 (Mitui et al., 1989). The most likely explanation of $n = 123$, given the morphological evidence that clearly indicates the plant is an *Asplenium*, is that the parents had the unusually high chromosome number of $n = 41$. The resemblance to *A. delitescens* suggests that that species is one of its parents; however, *A. delitescens* is not known from Trinidad (Map 2).

12. Asplenium delitescens (Maxon) L. D. Gómez × **A. laetum** Sw. Figure 6B.

The specimens listed below are presumably hybrids based on their intermediate morphology between *A. delitescens* and *A. laetum*.

Specimens examined. BELIZE. STANN CREEK: Stann Creek Railway, 50 m, *Schipp 49* (BM, MICH, MO, UC). COSTA RICA. ALAJUELA: Río Chiquito, ca. 40 km on road to Upala, 800 m, *Gómez 18620* (MO, UC). SAN JOSE: Zona Protectora El Rodeo, along Fila Diamante, S from Alto Gracias a Dios, 4 km (by air) SW of Ciudad Colón, 900 m, *Grayum & Zamora 9661* (MO, UC). VENEZUELA. ARAGUA: near Guamitas, Parque Nacional, 760 m, *Alston 5828* (MO). FALCON: Parque Nacional Quebrada de la Cueva El Toro, steep, wet valley along river, 600 m, *Liesner et al. 7724* (MO, NY, UC). COLOMBIA. BOLIVAR: Mpio. de San Jacinto, ca. 16 km NW of San Jacinto, N slope of Cerro Maco, 600 m, *Zarucchi & Cuadros 4040* (MO). MAGDALENA: 7 km E of Codazzi, 300 m, *Haught 3761* (COL, GH). META: La Macarena, Río Güejar ca. 10 km below junction with Río Zanza, 470 m, *S. G. Smith & Idrobo 1523* (COL, GH, UC). ECUADOR. MORONA-SANTIAGO: Cordillera de Cutucú, road Méndez–Morona, 800 m, *van der Werff & Palacios 10403* (F, MO, QCNE). NAPO: Parque Nacional Yasiní, Anangu, Río Anangu near junction with Río Napo, 270 m, *Luteyn et al. 8502* (NY, UC). PERU. HUANUCO: ca. pueblo de Puerto Inca, a unos 85 km de la confluencia con el Río Ucayali, 400–500 m, *Schunke V. 2967* (NY). LORETO: above Pongo de Manseriche, 250 m, *Mexia 6223* (BM). MADRE DE DIOS. Manú, Parque Nacional Manú, Pakitsa Station, Tachigali Trail to 8 km N of camp, 350 m, 11°56′S, 71°16′W, *Foster & Baldeón 12806* (F). BOLIVIA. BENI: Prov. Ballivián, Río Colorado, Collegio Técnico Agropecuario de Río Colorado, 235 m, 15°00′S, 67°10′W, *Fay 2078* (MO). LA PAZ. Prov. Larecaja, Isupuri, 500 m, *Williams 1091* (GH, NY); Prov. Nor Yungas, puente sobre el Río Beni, 550 m, *Beck 13367* (F).

The above specimens would key to *A. laetum* because of their number of pinna pairs (10–21) and atropurpureous petioles and rachises. These intermediates differ from *A. laetum* by their larger laminae and often abruptly contracted apices. The above specimens differ from *A. delitescens* in the shape of the lamina apices (especially the shape of the pinnae below the apical segment), greater number of pinna pairs, and dark petioles (Fig. 6B). The shape of the lamina apex is perhaps the best characteristic to detect the intermediates, but it is difficult to characterize the plants because of their inherent variability in features that distinguish the parents.

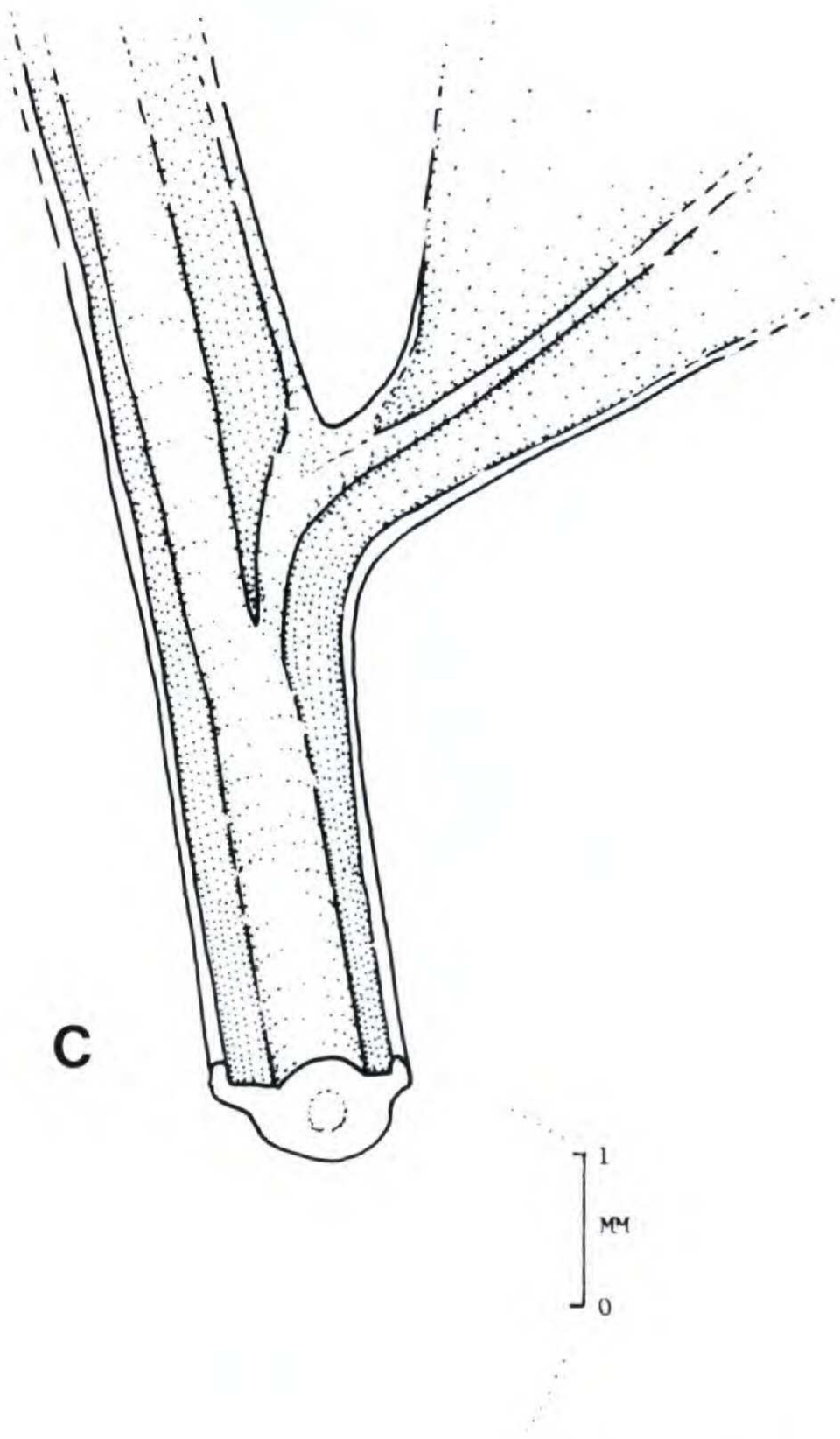
Most of the specimens have aborted spores, but some appear to have normal spores. The specimens treated here need to be investigated cytologically and enzymatically to confirm their hybridity and determine their parentage. A few may eventually be shown to have *A. ortegae* or *A. purpurascens* as the other parent.

13. Asplenium ×incisoserratum (Rosenstock) Murakami & R. C. Moran, stat. nov. *Asplenium laetum* Sw. var. *incisoserratum* Rosenstock, Repert. Spec. Nov. Regni Veg. 22: 8. 1925. TYPE: Costa Rica. San José: Grenadilla, 1,200 m, 26 Dec. 1910, *Brade 425* (holotype, S; isotypes, B, M, UC). Figure 16.

Plants epilithic; roots 0.1–0.5 mm wide; rhizome 2–4 mm wide, scaly at the apex; scales 2–2.5 × 0.25–0.35 mm, blackish, narrowly triangular to linear; petiole base 0.5–2 mm wide, swollen, 1–1.5 mm distant from each other on the same row; petiole 3–8 × 0.03–0.1 cm, ca. ⅕–⅓ the leaf length, mostly stramineous to greenish, sometimes brown basally (especially in large leaves), glabrous; lamina 8–20 cm long, green, 1-pinnate, lanceolate, gradually to abruptly tapered to a pinnatifid apex; rachis greenish; lateral pinnae 1.4 × 0.5–1 cm, 6–14 pairs, lanceolate, acute to obtuse, coarsely dentate, the teeth 1–2 mm deep, the basal basiscopic side excavate for ⅓–½ the length of the pinna; veins 1-forked; sori 3–5 mm long; spores irregular, aborted.

Additional specimens examined. MEXICO. OAXACA: Tuxtepec, above Jalapa de Díaz, 330 m, *Hallberg 1467* (NY). COSTA RICA. CARTAGO: Río Reventazón, below Turrialba, 540–600 m, *Skutch 4681* (CR, F, GH, MO). SAN JOSE: Río Surubres, 300 m, *Brade 430* (B, GH, M, S, UC); vic. of El General, 1,100 m, *Skutch 2531* (MICH, MO, S); basin of El General, 675–900 m, *Skutch 4790* (CR, MICH, MO). TRINIDAD. No locality, *Fendler 61 pro parte* (B, GH, MO). COLOMBIA. VALLE: valley of Río Digua, 950 m, *Alston 7837* (MO).

Asplenium ×incisoserratum grows on wet cliffs and boulders in streams from 300 to 1,200 m.



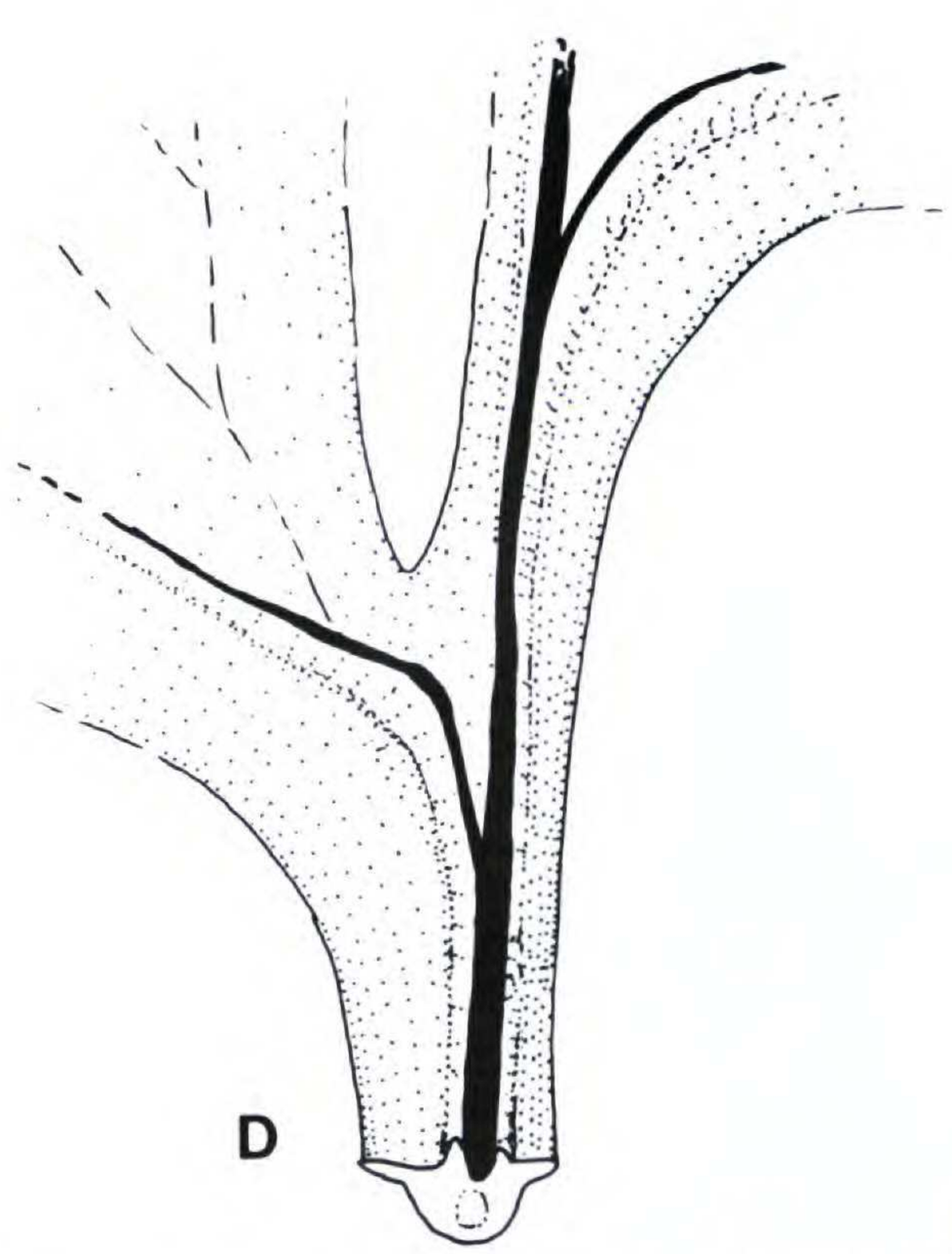


FIGURE 16. A, B. *Asplenium* ×*incisoserratum* (*Brade 430*, GH).—A. Large fertile leaf.—B. Small fertile leaf.—C. *A. abscissum*, juncture of rachis and pinna, note the raised, ungrooved rachis and costa, and thickened decurrent pinna margins (*Skutch 2339*, MO).—D. *A. delitescens*, juncture of rachis and pinnae, note the grooved rachis and the narrow wing that borders the costules and the rachidial groove (*Martínez S. 16399*, MO).

Based on morphology (Fig. 16), it appears to be a hybrid between *A. hoffmannii* and *A. laetum*. From *A. hoffmannii*, it differs by having more pinna pairs, more than two or three leaves per rhizome, and a basally darkened petiole (especially in large leaves). From *A. laetum*, it differs by its usually greenish petiole, greenish rachis, fewer number of pinna pairs, and more deeply and thoroughly incised-serrate pinnae. All of the specimens cited above have aborted spores.

Two miscellaneous notes: The specimen cited from Colombia appears to be this hybrid, but *A. hoffmannii* is not known from western Colombia where the specimen was collected. Apparently, Rosenstock (1925) did not publish a new name when referring to *Brade 430* as representing a "forma minor, die vorliegenden Exemplare fruktifizieren schon bei 6 cm Höhe." This diagnosis is in German, contrary to Rosenstock's varieties in the same paper, which are in Latin. Also, the typography of "forma minor" is in roman, not boldface or italic as he usually used when publishing new names.

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Index to Collectors' Names and Numbers

This monograph is based on the specimens cited below, which consist of about 1,800 herbarium sheets representing approximately 780 gatherings from 22 herbaria (see acknowledgments for list of herbaria). Types are in boldface. The numbers in parentheses refer to the number of the species and hybrids in this monograph, given below for easy reference.

SPECIES

1. A. delitescens (Maxon) L. D. Gómez
2. A. hoffmannii Hieron.
3. A. laetum Sw.
4. A. obtusifolium L.
5. A. ortegae Murakami & R. C. Moran
6. A. purpurascens Mett. ex Kuhn

7. A. repandulum Kunze
8. A. riparium Liebm.
9. A. triquetrum Murakami & R. C. Moran
10. A. volubile Murakami & R. C. Moran

HYBRIDS

11. A. ×papyraceum (Jermy & T. Walker) Murakami & R. C. Moran
12. A. delitescens × A. laetum
13. A. ×incisoserratum (Rosenstock) Murakami & R. C. Moran

Abbott 2627 (3). Acosta S. 13783 (3); 13815 (6). Aguayo 268 (9). Allen 347 (1). Alston 5828 (12); 7716 (3); 7837 (13); 8707 (3); 8868 (1); 8925 (1). Antonio 3530 (4). Argüello 498 (6). Asplund 5550 (10). Avilés 16 (1); 66 (3). Ayala 58 (6). Aymard C. 5274 (3); 5297 (3).

Baker & Zaruma 6476 (3). Baker et al. 5797 (8). Barber 6 (3); 2500 (3). Barrington 404 (8). Bartlett & Lasser 16580 (1); 16843 (2). Beck 13367 (12). Belanger 801 (4). Béliz 150 (3). Bell 200 (6); 238 (6). Bennett 20 (3). Bernoulli 347 (3); 834 (2). Bernoulli & Cario 290 (2). Bohs et al. 1701 (8); 1832 (8). Bourgeau 362 (8); 2014 (8); 2151 (3). Box 456 (4); 464 (3); 473 (4). Brade **425** (13); 430 (13); 765 (8); 5242 (9); 6528 (9); 8240 (9). Brandbyge & Asanza C. 31225 (5); 31649 (5). Breedlove 26082 (8); 29819 (8); 29935 (1); 32617 (8); 33123 (1); 33850 (1); 33853 (1); 33893 (2); 34197 (3); 35410 (8); 38081 (8); 39059 (3); 42851 (2). Breedlove & McClintock 34140 (1). Breedlove & Smith 21683 (3); 31319 (3). Brenckle 47-201 (8). Brenes 21520 (3). Britton & Wilson 5300 (3). Britton et al. 909 (3); 1656 (4). Broadway 3026 (3); 4212 (3); 5353 (4); 7180 (3). Brown 1338 (3). Buchtien **625** (9); 3334 (3); 3348 (9). Buchwald 43 (6). Bunting et al. 12036 (3). Burandt 715 (3). Burch 6114 (8). Burch et al. 1095 (1). Burger et al. 11916 (8).

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Davidse & González 19242 (1). Davidse et al. 18205 (5); 18826 (5); 28440 (8); 28518 (8). Deam 470 (1). de Granville 3508 (8). de Granville et al. 8947 (3). Dodson & Gentry 10051 (6); 12275 (6). Dodson et al. 7089 (1). Dorantes et al. 2555 (3). Dusén 3351 (9); 3551 (9); 6774 (9); 13730 (9). Duss 1635 (3); 1636b (4); 4199 (3); 4205 (4). Dwyer 6823 (2).

Edwall & Puttemans 5004 (9). Eggers 608 (4); 15118 (3); 15175 (3); 15214 (6). Ekman 2533 (1); 2760 (1); 4430 (3); 6106 (3); 7332 (3); 14338 (3); 15271 (3); 15485 (3); 15836 (3). Evoy 61 (3).

Fagerlind & Wibom 1593 (6). Fay 665 (3); 673 (4); 2078 (12). Fendler 61 (2 & 13); 131 (4); 136 (3); 139 (4); 143 (1). Finck 159 (1); 35 (8). Folsom 3062 (4); 9735 (8). Forero & Jaramillo 2134 (3). Forero et al. 6840 (10); 7237 (10). Foster 85-150 (8). Foster & Baldeón 12806 (12). Foster et al. 3449 (7).

Galeotti 6274 (8); 6275 (8). Gardener 168 (9). Gentle 2714 (1); 5139 (1); 6261 (1); 7378 (3). Gentry 8679 (1); 14069 (8). Gentry & Clewell 7064 (3); 7069 (3). Gentry et al. 23073 (7). Ghiesbreght 416 (8); 426 (3). Gilbert 54 (3). Gittins 4220 (8). Glaziou 5318 (3); 7247 (9); 7954 (9); 12283 (9); 12289 (9). Gómez 2168 (8); 18620 (12). Gómez et al. 19195 (10); 23094 (3). Grayum 8506 (8). Grayum & Hammel 5530 (8); 8466 (8). Grayum & Schatz 3140 (8). Grayum & Zamora 9661 (12). Grayum et al. 4419 (3); 4906 (3); 5060 (8); 5808 (8); 8943 (3); 9152 (3); 9159 (2). Grijalva 299 (8); 471 (8). Guzmán V. 553 (8).

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Imray 13 (4); 120 (3).

Jack 7093 (3). Jenman 24 (3). Jermy 2178 (11); 11370 (3). Jiménez M. 2816 (10). Johnston 74 (3); 131 (2); 161 (3); 258 (2); 385 (2); 444 (2). Jürgens 27 (3); 372 (9); 391 (9).

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